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LIFE HISTORIES OF STONEFLIES (PLECOPTERA) IN THE RIO CONEJOS OF SOUTHERN COLORADO

R. Edward DeWalt[1,2] and Kenneth W. Stewart[1]

ABSTRACT.—Thirty-one stonefly species representing eight families were collected during the March 1987 to May 1990 study period. Genera represented by more than one species included *Capnia, Utacapnia, Taenionema, Suwallia, Triznaka, Isogenoides,* and *Isoperla.* Peak species richness was recorded on or near the summer solstice in 1988 and 1989. Climatic differences between years were reflected in nymphal development and emergence phenology of most species. New or important corroborative life history data are presented for 11 stonefly species of this assemblage. The hyporheic nymphal development of most chloroperlid species limited the number of early instars sampled and our capacity to interpret voltinism. Limited nymphal data suggested a univoltine-slow cycle for *Plumiperla diversa* (Frison). Adults of *Suwallia pallidula* (Banks) and *S. wardi* (Banks) were present for an extended summer period, but the bulk of their respective emergence times was temporally separated. *Isogenoides zionensis* Hanson, *Pteronarcella badia* (Hagen), and *Pteronarcys californica* Newport were all shown for the first time to have a 9–10-mo egg diapause, and all three species have a semivoltine life cycle. *Skwala americana* (Klapálek) and *Isoperla fulva* Claassen were further confirmed to have univoltine-slow cycles. Univoltine-fast and univoltine-slow life cycles are reported for the first time in *I. phalerata* and *I. quinquepunctata,* respectively. Regression analysis revealed that six of the eight abundant species had extended emergence patterns (slopes of <5%/d), while only two had synchronous patterns. Warmer spring and summer temperatures in 1989 increased the slopes for five of the eight species studied, but did not change their synchrony designation. Nine of 11 abundant species advanced their median emergence date in 1989 over 1988. This and the higher slope values are consistent with a hurried nymphal development and narrower emergence period due to the warmer thermal regime of 1989.

Key words: Plecoptera, life history, biodiversity, life cycle, Rocky Mountains.

Stoneflies (Plecoptera) are one of the integral and often dominant insect orders in stream ecosystems; therefore, they are important as biological indicators, as fish food, and as part of the energy and nutrient economy of streams (Stewart and Stark 1988). Taxonomy of the North American fauna is now well known; however, information on their life histories, local species richness, and ecology is still poorly understood (Sheldon and Jewett 1967, Stewart and Stark 1988). Precise life histories are known for <5% of the more than 575 North American species, and knowledge of stonefly life histories and ecology in southern Rocky Mountain streams is sparse. This has limited our ability to increase understanding of ecological relationships between cohabiting stonefly species in this region.

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One objective of this study was to determine richness of the stonefly assemblage of the Rio Conejos of southern Colorado, a large drainage that has not been previously studied. Second, we documented the important life history events of its dominant species for which sufficient individuals and observations could be gathered by intensive monthly sampling and by living streamside during spring and summer.

Research was patterned after the classic studies of Harper (1973a, 1973b) and Harper and Hynes (1972), who studied a substantial portion of the eastern Canadian fauna and addressed critical aspects of life histories such as egg development, diapause, and adult behaviors that are often overlooked. H. B. N. Hynes, in an address to the International Plecoptera Symposium (1992), emphasized the need for more attention to these aspects to support the eventual development of a paradigm of life history evolution within the Plecoptera. We have also adopted the approaches of Knight and Gaufin (1966), Harper and Magnin (1969), Sheldon (1972), Barton (1980), Ernst and Stewart (1985a, 1985b), and Hassage and Stewart (1990) in comparatively studying an assemblage of species. This report is the first to address, on a large scale, such an assemblage in a western North American stream since the works of Knight and Gaufin (1966), Sheldon (1972), and Stanford (1975).

METHODS

Study Stream

The Rio Conejos is located in the southern Rocky Mountains of south central Colorado. The river flows east to west for 145 km from its headwaters in the Rio Grande National Forest of the San Juan range to the Rio Grande 32 km northeast of Antonito, CO. Three sampling sites were established along the Rio Conejos to ensure access to at least one of them during the winter and to enhance collection of stonefly species that were not abundant at all sites. These were located at elevations between 2400 and 2600 m above sea level. The primary site (106°15'W longitude, 37°03'N latitude) consisted of a 1-km stretch located 24 km west of Antonito, Conejos County, CO, off Colorado highway 17. Sites two and three were located 22.5 km west of Antonito, also on highway 17, and 4 km north of Antonito at the Colorado highway 285 bridge, respectively.

Stream temperatures varied from below freezing during the winter months to near 20°C in August. Ice cover was common from December through March. Snowmelt began in April, usually leading to peak flows in June. Base flows were attained by late August and continued through the winter. Water released from Platoro Reservoir, 48 km upstream, augmented river flow during summer low-flow periods. Bottom substrates were characterized by large boulders, cobble, gravel, and sand. These were covered by a thin layer of silt in quiet water. Important organic substrates included the flooded coppices of willows and cottonwoods and their entrained leaf packs. Willow (*Salix* spp.), cottonwoods and aspens (*Populus* spp.), and alder (*Alnus* sp.) contributed to the riparian corridor.

Physical Conditions

Stream temperature was monitored at site one from June through August 1988 using a Ryan™ continuous recording thermograph. High, low, and mean daily stream temperatures were calculated from temperatures recorded at 0400, 0800, 1200, 1600, 2000, and 2400 h. Water temperatures were not recorded during 1989 due to equipment failure. However, summer air temperature highs and lows and rainfall were recorded (1300 h daily, mountain time) for both 1988 and 1989 at the Conejos Peak U.S. Weather Service reporting station at site one. Flow data for site two were gathered from Petsch (1987–90).

Nymphal Growth

Nymphs were collected monthly (except December due to poor weather conditions) at all sites from March 1987 to May 1988. Additional collections were made at irregular intervals until March 1990. Samples were collected by disturbing the substrate (mineral and organic) upstream of a BioQuip rectangular dipnet until debris clogged the net. The net was composed of a coarse, 1-mm mesh first stage, modified by the addition of a conical second stage of 153-μm mesh size. The latter collected even the smallest instars. A plankton bucket was attached to the second stage to facilitate sample removal. Contents of the plankton bucket and the coarse stage constituted a sampling unit and were stored in

70% isopropyl alcohol. The number of sampling units per month varied with the effort necessary to secure approximately 50 nymphs of all abundant species.

Nymphs were separated from sample debris with the aid of 4–10X magnification on a stereo-dissecting microscope, sorted to species when possible, and stored in 80% ethanol until measurement. Head capsule width (HCW, greatest distance across the eyes) was measured with a calibrated ocular micrometer fitted to a stereo-dissection microscope. Nymphs from all sites for the 3-yr sampling period were pooled by species and month of collection to increase the number of nymphs per month and to allow construction of more robust growth histograms. Gender of nymphs was assessed by a gap in the posterior setal margin of the eighth sternum of females (Stewart and Stark 1988) and by developing external genitalia of females. Sex-specific kite diagrams were constructed by placing male and female nymphs into 0.1- or 0.2-mm size classes. The frequency of these classes was converted to a percentage of the total number of nymphs (males + females + unsexed nymphs) collected for that month. Polygons were constructed for each month depicting the relative proportion of all nymphs at that size class.

Adult Emergence

Adults of winter- and early spring-emerging stoneflies were collected from bridge abutments, from shoreline debris, and under the cobble at streamside to provide a general emergence period for each species. Adults were also reared from preemergent nymphs.

A combination of sampling methods and observational procedures was used during the summers of 1988 and 1989 to evaluate emergence, duration of adult presence, and behavior of these species. Adult traps and methods included a 2.25-m^2 basal area BioQuip malaise trap, two 0.25-m^2 basal area floating emergence traps, pitfall traps, sweepnetting of streamside vegetation, exuviae collection, and day and night transect walks. Pitfall traps were emptied on alternate days, and the others were emptied daily between 0900 and 1100 h. All of these methods were used at site one; sweepnetting was employed at site three on several occasions.

The malaise trap was deployed among willow and cottonwood coppices, where its olive-drab coloration mimicked the surrounding vegetation. Flying, or crawling, adults intercepted by the trap ascended the screening into a dry apical collection chamber. Additionally, all adults on the trap mesh were collected using an aspirator.

Emergence traps were anchored over shallow riffles during the 1988 field season. Natural diurnal changes in water level and erratic discharges due to water release from Platoro Reservoir rendered these ineffective at times; therefore, their use was discontinued in 1989.

Pitfall traps consisted of 28.3-cm^2 modified aluminum soda cans that were buried flush in streamside substrates. A mixture of 70% ethanol and ethylene glycol (the latter to retard evaporation) was used as a preservative. In 1988, 12 traps were installed 1 m from the stream at 1-m intervals on an open beach with nearby vegetation. This was expanded in 1989 to three transects, each consisting of 30 cans set 1 m apart in transects 1 m, 5 m, and 8 m from the initial shoreline. These traps monitored not only adult presence of ground-traversing, brachypterous stoneflies, but also their potential to move laterally from the stream.

Sweepnetting was conducted over a 15 × 2-m willow and cottonwood riparian zone. The entire area was methodically swept, working from the base of each clump of vegetation upward. Exuviae removal was the only method used to assess emergence of *Claassenia sabulosa* (Banks) and was used for no other species. In 1988 exuviae were removed daily from the same 15 × 1-m area of cobble shoreline, and the frequency of each sex was noted. In 1989 the removal area was expanded to 30 × 1 m of shoreline area and up to 5 m into the water for collecting exuviae from emergent substrates.

Year and sex-specific kite diagrams of adult presence were produced for all abundant summer stoneflies by pooling all methods and expressing daily catches as a percentage of the total catch. Duration of emergence of *Pteronarcys californica* Newport would be greatly overestimated by including pitfall trap collections due to its synchronous emergence and since pitfall traps were emptied on alternate days.

Dates of first capture, 50% cumulative catch, and last collection, plus total duration of adult presence, were determined for the 11 most abundant species collected in the summers of 1988 and 1989. Emergence synchrony was estimated using linear regression of the cumulative percentage catch (all methods pooled) versus days since first capture. Slopes generated for each species were used as an index of synchrony. Steeper slopes indicated a more synchronous emergence. Slopes ≥ 5%/d were chosen to be indicative of synchronous emergence since species with these slopes emerged their entire population within a few days and had steep, j-shaped, cumulative emergence curves. Differences between slopes for 1988 and 1989 were tested using a modified *t* test (Zar 1984). Common slopes were calculated if no differences between years were noted. This was a purely descriptive approach designed to detect and compare patterns; therefore, it is not our aim to model emergence for the purpose of prediction, but only to describe patterns of emergence.

Since most adult collection methods employed in this study collected adults of unknown age, results reflected adult presence rather than, in the strictest sense, emergence. No attempt was made to discard old males and females using any index of age. However, patterns of adult presence should follow that of a true emergence pattern, and since longevity of most adults approached only 1 wk in the laboratory, we believe these results to be useful.

Behavioral observations were made from 0800 to 1300 h and from 2000 to 2300 h for several days during emergence of each species. Observations made during intervening hours produced little adult behavior. Timing of adult activities, their relative distance from the stream, and substrates on which activities took place were monitored by walking the stream margin, turning logs and rocks, and exposing leaf-entrained bases of marginal vegetation. Details of these observations have been narratively described for each species in this paper.

Fecundity and Egg Incubation

Eggs of several species were incubated in the laboratory to confirm proposed voltinism based on growth histograms. Eggs were placed into 1-cm-diameter dialysis tubing bags and reared in a Frigid Units Living Stream™, or they were stored in 100 × 15-mm plastic petri dishes in an environmental chamber. In both instances these were incubated at approximate stream temperature and light regime.

Fecundity was estimated from number of egg batches deposited, number of eggs per batch, and, for *Skwala americana* (Klapálek) only, total number of eggs remaining in the ovarioles. Females were housed at streamside in screened, glass containers and provided with moist cotton balls as a source of water. Alternatively, some species were reared in Denton and held under simulated streamside conditions in large cotton-stoppered shell vials.

RESULTS

Physical Conditions

Mean daily stream temperatures in 1988 increased from near 10°C in early June to 15°C in mid-July (Fig. 1). The stream cooled dramatically between 8 and 12 July. This coincided with cool, damp weather conditions (Fig. 2). Summer air temperature highs rarely exceeded 30°C in 1988, and rainfall occurred at regular intervals throughout the summer (Fig. 2). However, 1989 was marked by many days above 30°C with rainfall relegated to late July and August (Fig. 2). The mean monthly discharge of the Rio Conejos during 1987–1989 fluctuated predictably. Peak discharge occurred typically in June but occurred in May during the warm, windy spring of 1989 (Fig. 3).

Species Richness

More than 13,000 nymphs and adults were studied over the 3-yr period. Among these

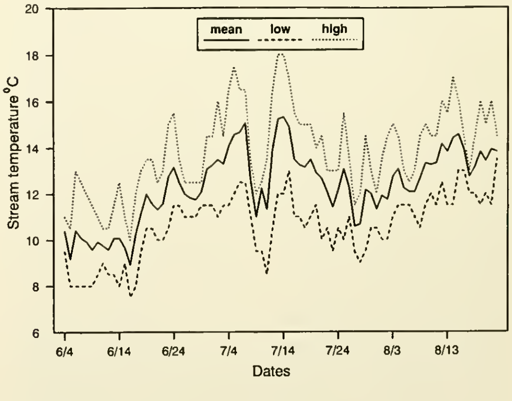

Fig. 1. Daily mean, high, and low stream temperatures in the Rio Conejos, summer 1988.

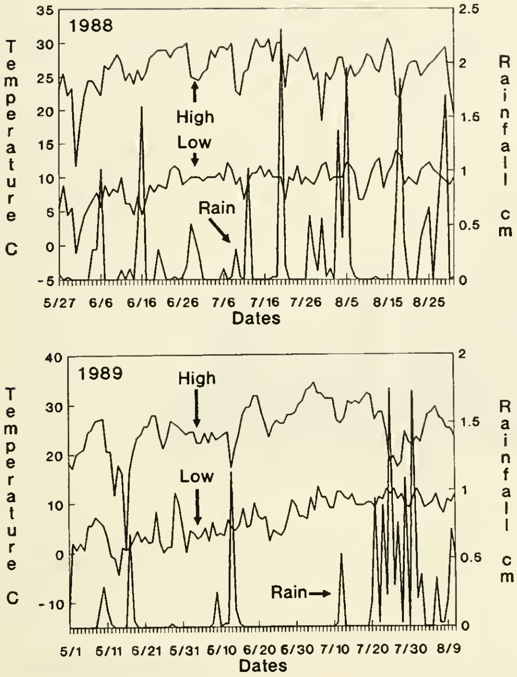

Fig. 2. Daily high and low air temperatures and rainfall for summer 1988 and 1989.

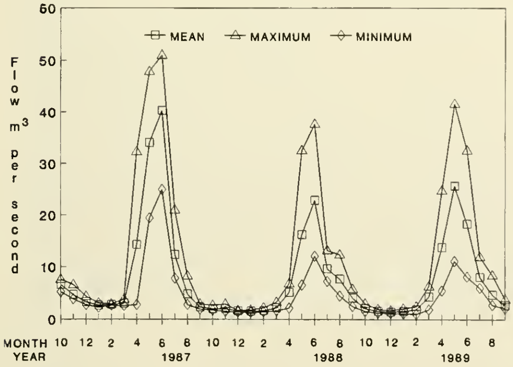

Fig. 3. Mean, minimum, and maximum monthly stream discharge of the Rio Conejos during the study period.

were 31 species (Table 1) in eight families. The Chloroperlidae, Perlodidae, and Capniidae were the most speciose families with six, seven, and seven species, respectively. Seven genera were represented by more than one species: *Capnia, Utacapnia, Taenionema, Suwallia, Triznaka, Isogenoides,* and *Isoperla* (Table 1).

Peak species richness occurred on or near the summer solstice in both years (Fig. 4). Pattern differences existed between years, including an early waning and a more peaked distribution of species richness in 1989.

Leuctridae

***Paraleuctra vershina* Gaufin and Ricker.** This was the only leuctrid found at our sites. No nymphs were recovered from the stream, indicating a probable hyporheic existence. Adults were abundant in riparian vegetation during June and July (Fig. 5). No variation in adult presence parameters was noted for *P. vershina* (Table 2). Emergence was classified as extended in both years, although slopes of these cumulative emergence curves were significantly different over the 2 yr (Table 3).

TABLE 1. Stoneflies collected from the Rio Conejos, Colorado, March 1987 through March 1990.

Euholognatha
- CAPNIIDAE
  - *Capnia coloradensis* Claassen[1]
  - *Capnia confusa* Claassen
  - *Capnia vernalis* (Newport)
  - *Isocapnia crinita* (Needham & Claassen)[1]
  - *Utacapnia logana* (Nebeker & Gaufin)[1]
  - *Utacapnia poda* (Nebeker & Gaufin)[1]
- LEUCTRIDAE
  - *Paraleuctra vershina* Gaufin & Ricker[1]
- NEMOURIDAE
  - *Amphinemura banksi* Baumann & Gaufin[1]
  - *Prostoia besemetsa* (Ricker)[1]
  - *Zapada frigida* (Claassen)[1]
- TAENIOPTERYGIDAE
  - *Taenionema pallidum* (Banks)[1]
  - *Taenionema pacificum* (Banks)[1]
  - *Doddsia occidentalis* (Banks)[1]

Systellognatha
- CHLOROPERLIDAE
  - *Paraperla frontalis* (Banks)[1]
  - *Plumiperla diversa* (Frison)[1]
  - *Suwallia lineosa* (Banks)[1]
  - *Suwallia pallidula* (Banks)[1]
  - *Suwallia wardi* Kondratieff & Kirchner[1]
  - *Triznaka pintada* (Ricker)[1]
  - *Triznaka signata* (Banks)[1]
- PERLIDAE
  - *Claassenia sabulosa* (Banks)[1]
  - *Hesperoperla pacifica* (Banks)[1]
- PERLODIDAE
  - *Isogenoides zionensis* Hanson[1]
  - *Isogenoides* prob. *colubrinus* (Hagen)[1]
  - *Isoperla fulva* Claassen
  - *Isoperla mormona* Banks[1]
  - *Isoperla phalerata* (Smith)[1]
  - *Isoperla quinquepunctata* (Banks)
  - *Skwala americana* (Klapálek)
- PTERONARCYIDAE
  - *Pteronarcella badia* (Hagen)
  - *Pteronarcys californica* Newport[1]

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[1] New drainage and county records.

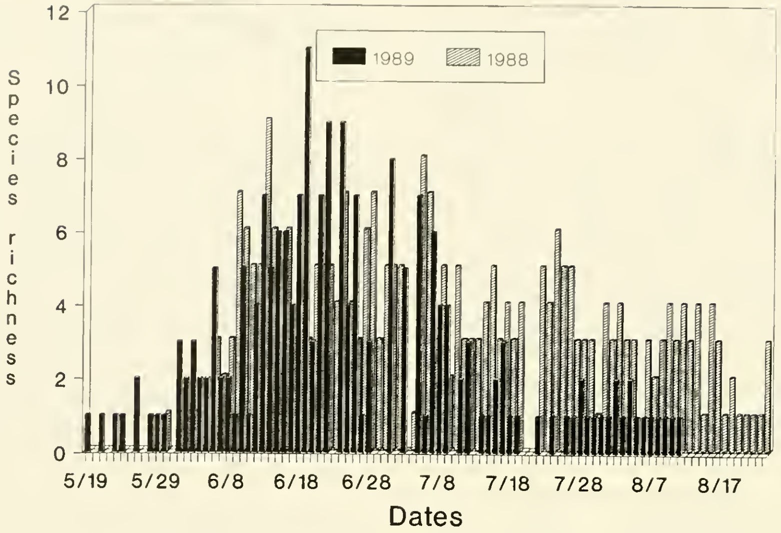

Fig. 4. Temporal species richness pattern of adult stoneflies collected daily from the Rio Conejos during the summers of 1988 and 1989.

Chloroperlidae

Representatives from two subfamilies inhabited the stream. The early- and mid-instar nymphs of the Chloroperlinae genera could not be reliably identified to genus. This necessitated the illustration of a portion of the nymphal growth of *Plumiperla diversa* (Frison) and *Triznaka signata* (Banks) as Chloroperlinae spp. (Fig. 6). Growth of reliably identified mid- to late-instar nymphs was illustrated separately.

Paraperla frontalis **(Banks) (Paraperlinae).** Nymphs were collected infrequently among marginal substrates during the colder months of the year. All were pale, very thin, and had eyes set far forward as described for mature nymphs (Stewart and Stark 1988). These limited data are presented for the first year of the presumed semivoltine growth pattern of this large chloroperlid (Fig. 6). Less than 10 adults were collected in early June during the 3-yr study.

Plumiperla diversa **(Chloroperlinae).** No adults were collected on which to base specific identity; however, nymphs of this genus are distinctive, and only *P. diversa* has been collected in this region (Baumann et al. 1977). Nymphs were identifiable to genus by March. Females were readily distinguished from males at this time. Growth continued through May when females attained a median HCW 9.6% larger than males. The limited nymphal data suggested a univoltine-slow life cycle for this species.

Suwallia pallidula **(Banks) (Chloroperlinae).** Only 59 nymphs of *Suwallia* spp. were collected from the Rio Conejos, even though adults were abundant. Nymphs were hyporheic until immediately prior to emergence. This habitat preference and our present inability to distinguish congeners of *Suwallia* nymphs precluded generation of meaningful histograms and designation of voltinism for either species. Adults of *Suwallia wardi* Kondratieff & Kirchner were consistently larger than *S. pallidula*. This trend followed in nymphs, too, with proposed female nymphs of *S. wardi* in June (peak emergence) being 22.0% larger

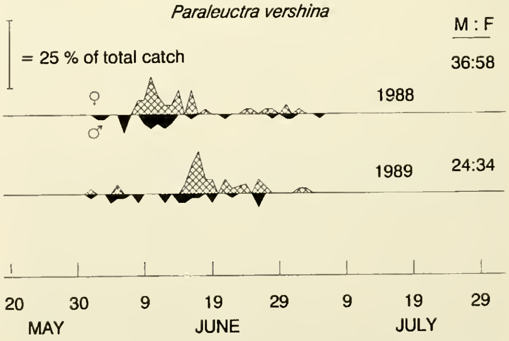

Fig. 5. Emergence of *Paraleuctra vershina* from the Rio Conejos, 1988 and 1989. Polygons indicate daily relative proportion of total catch.

TABLE 2. Range of dates for adult presence parameters for 11 summer-emerging stonefly species collected in 1988 (appears first) and 1989 from the Rio Conejos. Duration is mean ± SD of the number of days. All parameters not available for *C. sabulosa,* which emerged past our study period.

Species	*n*	Date 1st capture	Date 50% catch	Last date capture	Duration (d)
P. vershina	94	2 June	12 June	5 July	35.0 ± 0.0
	58	1 June	17 June	7 July	
S. wardi	467	6 June	10 July	15 August	66.0 ± 7.1
	352	19 May	25 June	18 July	
S. pallidula	276	30 June	28 July	23 August	44.5 ± 4.8
	162	1 July	14 July	4 August	
T. signata	662	9 June	28 June	23 August	59.0 ± 24.0
	2697	2 June	19 June	12 July	
C. sabulosa	356	19 July	—	—	—
	1195	16 July	—	—	—
I. fulva	19	9 June	22 June	7 July	24.5 ± 7.8
	61	9 June	18 June	28 June	
I. phalerata	12	20 June	28 June	24 July	22.5 ± 3.5
	20	18 June	25 June	8 July	
I. quinquepunctata	9	24 June	14 July	27 July	30.0 ± 4.2
	12	19 June	5 July	15 July	
I. zionensis	200	8 June	19 June	28 June	15.5 ± 4.9
	75	10 June	17 June	24 June	
P. badia	215	10 June	22 June	17 July	34.5 ± 3.5
	480	7 June	20 June	7 July	
P. californica	55	6 June	8 June	12 June	6.0 ± 2.8
	21	4 June	5 June	13 June	

than the July (peak emergence) females of *S. pallidula.* Only two proposed male nymphs of the latter were collected over the 3-yr period.

Adults of *S. pallidula* were collected in July and August in both years (Fig. 7, Table 2). Slopes from regression models were different between years (t = –64.7, $p < .0001$), but below the 5%/d criterion. We categorized this species as an extended emerger (Table 3). The median emergence date was advanced by 2 wk in 1989 over that of 1988 (Table 2). The adult sex ratio over the two seasons was 13 ♂: 415 ♀. Six field-collected and laboratory-maintained females produced only one egg batch (Table 4).

Suwallia wardi **(Chloroperlinae).** This was the most abundant of the three *Suwallia* species collected from the Rio Conejos. Adults were first collected in late May or early June, reached 50% cumulative catch by mid-July, and disappeared from streamside by early August (Table 2). It had the longest mean duration of presence (66 d) for any stonefly studied on the Rio Conejos (Table 2). Like its congener, *S. wardi*'s 1989 date of median catch was advanced by 2 wk over that of 1988 (Table 2, Fig. 7). Emergence of *S. wardi* was extended, and no significant slope differences were noted between years (Table 3). No egg data were collected for this species.

Riparian vegetation was used by this large, yellow-green chloroperlid as a staging ground for adult behaviors. *Suwallia wardi* was active throughout the morning on sunny days and again for 2–3 h before sunset if conditions were warm and dry. During cool, rainy days the low vegetation was devoid of *S. wardi* or any other stonefly species.

Triznaka signata **(Banks) (Chloroperlinae).** Identifiable, late-instar nymphs were collected during a 5-mo period in the spring and summer. Nymphs of this univoltine-slow

TABLE 3. Synchrony and linear regression statistics for the years 1988 (appears first) and 1989. Slopes between years were tested: * = significance .05–.01, ** = <.001 level or lower probability, and NT = not tested.

Species	Slope	R^2	p	Synchrony
P. vershina	3.0	.85	.0001	extended
	3.5^{**}	.90	.0001	extended
T. signata	1.5	.87	.0001	extended
	3.0^{**}	.91	.0001	extended
S. pallidula	2.5	.96	.0001	extended
	3.5^{**}	.90	.0001	extended
S. wardi	2.2	.84	.0001	extended
	2.2	.85	.0001	extended
C. sabulosa	2.8	.94	.0001	extended
	4.1^{**}	.99	.0001	extended
I. zionensis	7.5	.92	.0001	synchronous
	7.9	.95	.0001	synchronous
P. badia	3.6	.81	.0001	extended
	4.4^{*}	.92	.0001	extended
P. californica	13.3	.84	.004	synchronous
	18.9^{NT}	.97	.103	synchronous

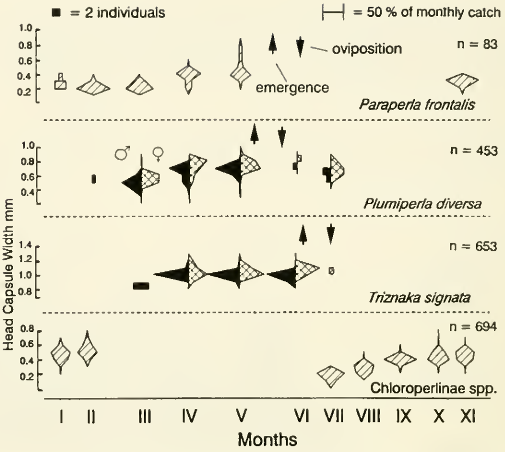

Fig. 6. Growth of Chloroperlidae nymphs collected from the Rio Conejos, 1987–1990.

species were largely full grown by April (Fig. 6) with some degree of sexual dimorphism present at this time.

Adults first appeared in early June, reached 50% cumulative catch 2 wk later, and could no longer be collected by late August (Fig. 7, Table 2). Emergence was protandrous, but slightly female-skewed sex ratios dominated in both 1988 and 1989 (Fig. 7). *Triznaka signata* displayed the greatest variation in last date of capture and duration of presence of all stoneflies in the river (Table 2). It advanced its 1989 median emergence date by 9 d over that of 1988. Regression slopes indicated an extended emergence in both years (Table 3). Differences between slopes for 1988 and 1989 were significant ($t = -11.35$, $p < .0001$).

Attempts during the entire study to obtain eggs from laboratory-reared and -mated females were unsuccessful. The mean number of eggs from six females caught during oviposition flights was lower than any first batches for other stoneflies studied (Table 4). Although these females were held for a prolonged period of time, no additional egg batches were laid.

Adults were never seen emerging in the field, despite many hours of observation along the shoreline, day and night, in habitats where they were collected in abundance during the day. Adults inhabited marginal vegetation, where males were observed actively searching willow stems and leaves for females. No drumming was observed during the two summers of intensive fieldwork. Large flights of adults of both sexes took place just before dark, at which time females were observed ovipositing. Egg masses were dropped from up to 4–5 m above the stream.

Perlidae

Claassenia sabulosa. Although two perlids were present in the Rio Conejos (Table 1), only *C. sabulosa* was sufficiently abundant for growth and emergence interpretation. Nymphs of this species were found among larger rubble of midstream. The life cycle was semivoltine and appeared to require 3 yr of nymphal growth (Fig. 8). Recruitment occurred throughout the fall with possibly some additional recruitment in March from overwintering eggs. Eggs containing eyespots were recovered from the stream in October and November. Sexual dimorphism in both size and external genitalia occurred when nymphal size reached 2.2 mm HCW. The size disparity increased until the third year of growth when little overlap between the sexes remained.

A protandrous emergence began in mid-July in both years (Fig. 9, Table 2). Exuviae of this species were abundant throughout August, possibly into September. Emergence of *C. sabulosa* was extended and slopes were significantly different between years ($t = -10.7$, $p < .0001$, Table 3).

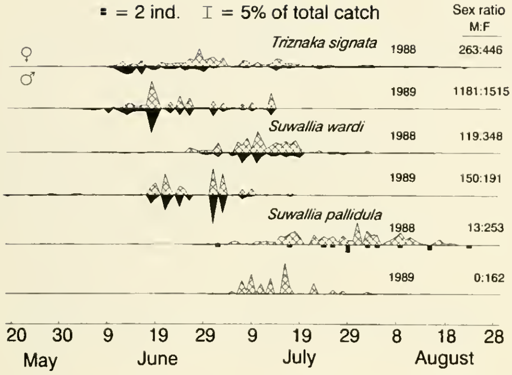

Fig. 7. Emergence of Chloroperlidae from the Rio Conejos, 1988 and 1989. Polygons indicate daily relative proportion of total catch.

Claassenia sabulosa produced the greatest mean number of eggs of any stonefly species studied (Table 4), with females producing up to four batches. Longevity of seven females was 3.9 ± 1.9 d. Egg production lasted through 80% of the adult life. Several egg batches were incubated, but none hatched within 6 mo of observation.

Emergence occurred between 2000 and 2200 h. Nymphs crawled out of the water onto emergent cobble and boulders to transform, the entire molting process taking less than 5 min. Hardened and newly transformed males ran over all emergent substrates, searched for females in a circular pattern, and drummed mostly on large mineral substrates. Pitfall trap collections of 1989 caught a total of 115 male adults in transect 1 and only 12 in transects 2 and 3. Only two females were collected in the pitfall traps, presumably because of their less-intensive and unidirectional movement pattern. Therefore, excursions of great distance away from the water's edge for either sex were infrequent. Females were often found in the morning under dry cobble with abdomens devoid of eggs or with large egg masses suspended between the cerci. Several females were observed at night running over the surface of the water, but the cause of this behavior could not be determined. No females were actually observed ovipositing. Males were distinctly cursorial, which fits with their brachypterous morphology; however, females were never observed flying, nor did they inhabit tall substrates, even though they had full wings.

Perlodidae

***Isogenoides zionensis* Hanson (Perlodinae: Perlodini).** The large range in size of nymphs from July samples (Fig. 10) could not be accounted for by nymphs hatching from eggs laid by June-mated females. June eggs reared at simulated stream conditions hatched in March and April, 9–10 mo after oviposition. Therefore, at least some individuals of this species have a semivoltine life cycle with eggs diapausing over their first summer and winter. Early-instar nymphs were missed in benthic samples during their second spring, possibly due to high water or their occurrence deep in the substratum. Sexual dimorphism in size and morphology was apparent by July of the second year when nymphs approached 1.8 mm HCW (Fig. 10). This disparity increased steadily throughout the rest of their growth. Little overlap in size of the sexes existed by May prior to emergence.

The adult presence parameters of *I. zionensis* showed little variation over the 2 yr studied (Table 2). Emergence was not protandrous, but the sex ratio was heavily skewed towards males (Fig. 11). This species was one of two that emerged synchronously (Table 3). No difference in slope was found between years ($t = 0.82$, $p > .2$); therefore, a common slope of 7.6%/d was calculated.

Laboratory-reared females put nearly 75% of their total egg complement into a first batch (Table 4). Only one of four females produced additional batches.

Transformation of *I. zionensis* took place from 2030 to about 2200 h. Nymphs crawled away from the stream until they reached willows or other vegetation, then ascended <1 m vertically where they molted. Daylight activity began by 0700–0800 h at the base of small willow coppices, where adults were often found in emergent leafpacks. Adults ascended streamside willows as the sun rose. Drumming, mating, and egg batch formation took place from these perches. Females crawled to the tops of these willows and flew to the stream where they fluttered on the water to release their black egg masses. Most activity ceased by 1300–1400 h on days when air temperature reached near 25°C. On cloudy, cool days this ascendance did not occur. Most adults could then be found in the leaf-entrained bases of riparian vegetation. Drumming on willow stems

TABLE 4. Mean eggs per batch, number of batches, and mean total egg complement for nine species of stoneflies occurring in the Rio Conejos, Colorado.

	Eggs / batch *n*				
Species	1	2	3	4	Total
S. pallidula	54.7 ± 26.6 6	—	—	—	54.7 ± 26.6 6
T. signata	42.2 ± 17.4 6	—	—	—	42.2 ± 17.4 6
C. sabulosa	2166.0 ± 774.0 7	902.0 ± 246.2 5	158.0 ± 91.0 5	40.0 1	3188.0 ± 613.0 7
I. zionensis	588.0 ± 86.0 4	327.0 1	185.0 1	—	843.2 ± 141.4 4
I. fulva	231.5 ± 7.8 2	—	—	—	231.5 ± 7.8 2
I. phalerata	703.0 1	—	—	—	703.0 1
S. americana	884.7 ± 267.3 6	—	—	—	884.7 ± 267.3[a] 6
P. badia	339.0 ± 86.0 30	58.4 ± 37.2 5	56.8 ± 39.7 4	—	351.0 ± 101.0 30
P. californica	393.0 ± 125.6 4	191.3 ± 130.2 4	94.3 ± 49.5 4	69.8 ± 24.7 4	
	5	6	7		
	51.3 ± 29.3 4	58.5 ± 23.3 2	57.0 1		845.3 ± 90.5 4

[a]Total fecundity includes those eggs remaining in ovarioles.

was observed at night, even when temperatures approached 10°C.

***Isoperla fulva* Claassen (Isoperlinae).** We collected this species in benthic samples only occasionally, but enough individuals were obtained to allow a tentative interpretation of voltinism. Recruitment of nymphs was first detected in August (Fig. 12). These measured 0.4–0.8 mm HCW and grew at a slow rate throughout the fall until a winter decrease in growth rate. Their size increased dramatically after February, until emergence in June and July. This species conformed to a univoltine-slow growth pattern.

Adults were collected for the first time on 9 June in both years (Fig. 11, Table 2). Sex ratios for the small number of 1988 adults were approximately equal, but heavily skewed towards males in 1989. Numbers of adults collected in both years were too small to warrant an analysis of synchrony.

Fecundity was difficult to assess since few mature nymphs were available for rearing. One egg batch from each of two field-ovipositing females was collected (Table 4). Longevity of three field-collected adult females was 5.7 ± 0.58 d.

***Isoperla phalerata* (Smith) (Isoperlinae).** Although the number of nymphs collected was small, no month supported more than one size class (Fig. 12). Therefore, we have tentatively proposed a univoltine-slow growth pattern for this species. Adults were taken from mid-June through mid-July (Table 2, Fig. 11). No assessment of synchrony was made for *I. phalerata* due to low numbers of adults captured. Females did not produce eggs in captivity. A single egg batch from a field-collected individual contained 703 eggs. Four field-caught females lived 11.3 ± 3.6 d past date of capture.

***Isoperla quinquepunctata* (Banks) (Isoperlinae).** This species was more common at site

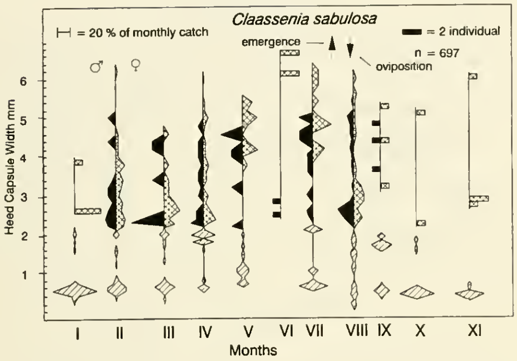

Fig. 8. Growth of *Claassenia sabulosa* nymphs collected from the Rio Conejos, 1987–1990.

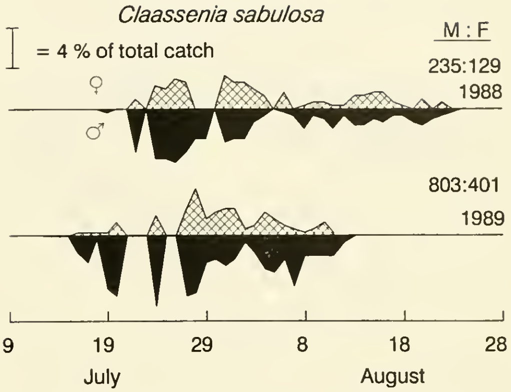

Fig. 9. Emergence of *Claassenia sabulosa* from the Rio Conejos, 1988 and 1989. Polygons indicate daily relative proportion of total catch.

three. The data suggested that *I. quinquepunctata* had a univoltine-fast growth pattern. Recruitment occurred in January and February (Fig. 12), and growth was rapid from March through May. Sexual dimorphism in nymphal size was not as evident in this species as in its congeners. Emergence began in mid-June and lasted through much of July (Table 2, Fig. 11). No eggs were collected.

***Skwala americana* (Klapálek) (Perlodinae).** This species displayed a univoltine-slow growth pattern and grew faster during summer and fall months than all other perlodids in the Rio Conejos (Fig. 13). Nymphs were recruited in June and increased their median HCW from 0.4 mm to about 2.8 mm by January. Growth was nearly completed by this time. Sexual dimorphism was apparent as early as August, and female nymphs reached a median HCW before emergence that was 21.4% greater than males. Female nymphs in April were found to contain fully sclerotized eggs in their oviducts; hence, this species is fully capable of mating and egg-laying immediately upon emergence.

Emergence was in April and early May when our sampling was still on a monthly basis; therefore, no detailed analysis of emergence phenology and synchrony can be offered. Adults were collected mainly from emergent logjam debris or under cobble at the stream margin.

Egg batches collected in mid-April from four laboratory-reared females hatched synchronously after a mean of 61.0 ± 7.3 d. This corroborates field collections of early-instar nymphs in June. Only a single egg batch was collected from each of six laboratory-reared females (Table 1).

Pteronarcyidae

***Pteronarcella badia* (Hagen).** This species was found to have a semivoltine growth pattern. Recruitment of nymphs began in March and April from eggs laid the previous June (Fig. 14). Many small nymphs were available in benthic samples by mid-April when they were at 0.2–0.4 mm HCW. This scenario was corroborated by laboratory incubation of several egg batches that hatched in March and April after a 9–10-mo diapause. Growth of nymphs was rapid throughout their first spring. Size differentiation among sexes was not apparent until August, a full 14 mo after oviposition. Median size of females just before emergence the following May was 21% greater than that of males.

Emergence began by early June, with slight protandry and a preponderance of males being collected (Fig. 15). Median emergence occurred in the third week of June in both years (Table 2). Emergence was extended (Table 3) and slopes were significantly different between years ($t = -2.2, p < .05$).

Females generally laid only single egg batches, but a small number produced up to three egg batches (Table 4). Most females laid their first egg batch within 24 h of mating and often waited 2-d intervals before laying others. Longevity of seven females under simulated field conditions was 7.7 ± 4.2 d.

Pteronarcella badia emerged just after dusk and typically used willows, cottonwoods, and stream margin sedges as transformation sites. Males were observed actively searching the willows and drumming for females at night,

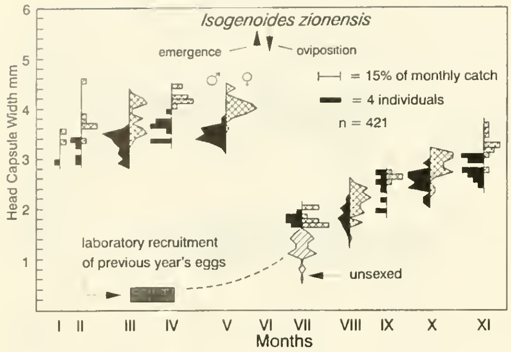

Fig. 10. Growth of *Isogenoides zionensis* nymphs collected from the Rio Conejos, 1987–1990.

even when air temperatures were near 10°C. Adults entered the leaf-choked bases of willows as the night progressed and were often found the next morning in large mating aggregations under these debris. These individuals ascended the willows as the sun warmed the air at streamside. Drumming, mate searching, mating, and egg batching took place in midmorning hours, while most activity ceased by 1200 h when air temperatures reached 22–25°C. Females oviposited by launching themselves from the tips of tall riparian shrubs toward the stream, where they would jettison their white egg mass a few meters above the surface of fast-flowing water.

***Pteronarcys californica* Newport.** This species is commonly known as the salmonfly. Recruitment began in April (Fig. 16) after a 9–10-mo egg diapause. Nymphs grew to only about 1 mm HCW through their first year. Sexual differences in size and morphology were apparent by June of their second year, when they were nearly 1.5 mm HCW. Nymphs grew for two more years, by the end of which time preemergent females had attained a 20% larger median HCW than males. These data suggest a semivoltine life history of 4-yr duration for this species.

Adults were first found on 6 June during both years (Fig. 15, Table 2). Emergence was a highly synchronous event (Table 3). Slopes were not tested for significant differences due to small sample size.

Most laboratory-reared females produced five egg batches, but one individual produced seven (Table 4). Egg production lasted through 82% of the 15.0 ± 1.8 d ($n = 4$) average adult female life span.

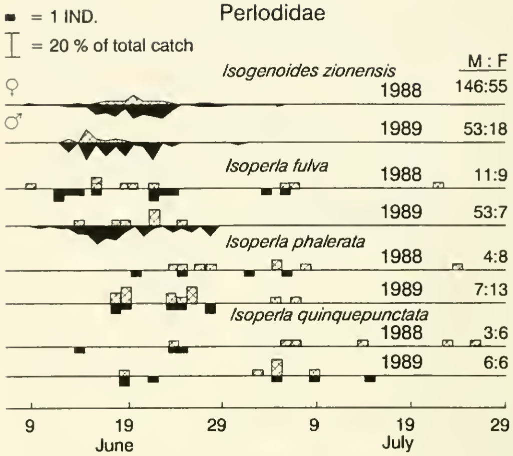

Fig. 11. Emergence of Perlodidae from the Rio Conejos, 1988 and 1989. Polygons indicate daily relative proportion of total catch.

Adults utilized marginal vegetation, much as did *P. badia*, as a staging ground for mating and ovipositing. However, they tended to select the taller cottonwoods and Engelmann spruce rather than the shorter willows for their activities. Salmonflies oviposited by flying over the stream and dropping their salmon-colored or bluish egg masses (dimorphism in egg color was observed) from as high as 10 m. Ovipositing adults were heavily fed upon by opportunistic Eastern Robins (*Turdus migratorius*) and Steller's Jays (*Cyanocitta stelleri*).

DISCUSSION

Species Richness

The Rio Conejos displayed a great diversity of Plecoptera. Twenty of the 31 species were evenly distributed among the Capniidae, the Chloroperlidae, and the Perlodidae. The only North American family not represented was the Peltoperlidae, which occurs transcontinentally, but not in latitudes below the northern Rocky Mountains (Baumann et al. 1977). Nearly all species collected were adapted for a montane existence and were characteristic of streams with high biotic integrity. Twenty-five species were both new drainage and county records (Baumann et al. 1977, Szczytko and Stewart 1979, Nelson and Baumann 1989; Table 1), though all of them had been previously reported from Colorado and neighboring New Mexico. This demonstrates that we have yet to adequately investigate the fine-scale diversity

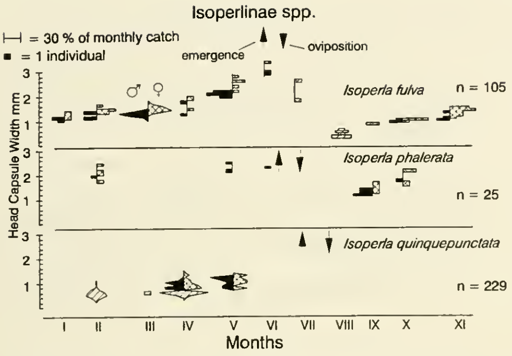

Fig. 12. Growth of *Isoperla* spp. nymphs collected from the Rio Conejos, 1987–1990.

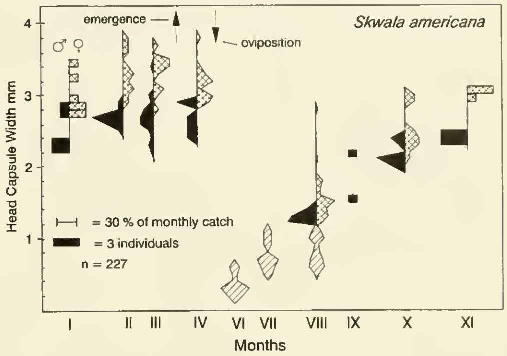

Fig. 13. Growth of *Skwala americana* nymphs collected from the Rio Conejos, 1987–1990.

and distribution of this order of aquatic insects in at least some portions of the southern Rocky Mountains.

Responses to Altered Thermal Regime

We became aware of substantial climatic differences (Fig. 2) between the two summers when adults were intensively studied. Though no water temperatures were available for 1989, air temperatures (Fig. 2) and hydrologic data (Fig. 3) suggested that the stream warmed more quickly and attained peak summer highs much earlier than in 1988. Consequently, development of several species was hurried, which narrowed the window of time adults were present streamside. At the assemblage level of organization, this trend is demonstrated by the species richness pattern of Figure 4. The 1989 pattern was more peaked and greatly truncated over that of 1988. Species-level responses can be demonstrated by inspection of the flight diagrams for each species. Nine of the 11 species presented in Table 2 show increased median emergence dates. Additionally, slopes produced by linear regression that were different between years (Table 3) were always higher in 1989. This result was consistent with a hurried nymphal development and shorter emergence period for each species.

Life History Parameters

LEUCTRIDAE

Paraleuctra vershina. Harper (1973b) reports that most *Leuctra ferruginea* in an Ontario stream are semivoltine, but that some univoltine individuals exist. Huryn and Wallace (1987) propose a 2-yr life cycle for a composite of *Leuctra* spp., most of which were probably *L. ferruginea* (Walker). Snellen and Stewart (1979) record univoltine fast cycles for *Zealeuctra claasseni* and *Z. hitei* in streams of north Texas. Additionally, Ernst and Stewart (1985a) report *Leuctra tenuis* as univoltine-fast in an Ouachita Mountain stream.

CHLOROPERLIDAE

Most Chloroperlidae exhibit a univoltine-slow or -fast growth pattern. *Haploperla brevis* (Banks) is widespread from Oklahoma to Quebec and west to Alberta, Canada. Ontario (Harper and Magnin 1969), Quebec (Harper et al. 1994), and Oklahoma (Ernst and Stewart 1985a) populations exhibited univoltine-fast growth with a 2–5-mo diapause, while Alberta populations were univoltine-slow (Barton 1980). European populations of *Chloroperla tripunctata* (Scopoli) (Elliott 1988), *Siphonoperla torrentium* (Pictet) (Elliott 1967), and *S. burmeisteri* (Pictet) (Benedetto 1973) also exhibited univoltine-slow growth. Species with semivoltine growth include *Sweltsa onkos* (Ricker) and possibly *Utaperla gaspesiana* Harper and Roy (Harper 1973a, Harper et al. 1994), *S. mediana* (Banks) (Cushman et al. 1977), and *S. lateralis* (Banks) (Huryn and Wallace 1987).

Paraperla frontalis. Stanford and Gaufin (1974) presented some evidence for semivoltine growth of this species. Emergence for this species and for *P. wilsoni* Ricker occurs from May through July (Stewart and Stark 1988). Paraperlinae are rather robust chloroperlids that tend to be hyporheic for most of their nymphal development. Their larger size, the more stable stream temperatures in the hyporheic environment (Hendricks 1993), and the possibly low availability of some nutrients in the

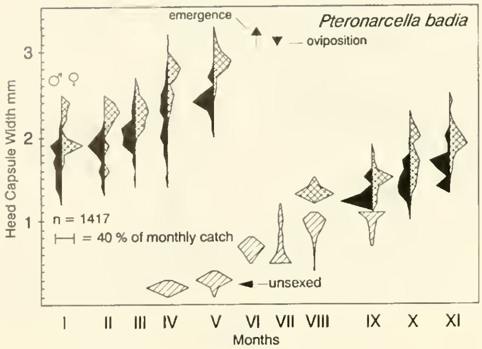

Fig. 14. Growth of *Pteronarcella badia* nymphs collected from the Rio Conejos, 1987–1990.

hyporheic habitat (Stanford and Ward 1993) may have contributed to a preponderance of semivoltinism in this subfamily.

Plumiperla diversa. Stewart et al. (1990) reported a univoltine-slow cycle for this species on the North Slope of Alaska. Emergence occurred from May through September, with recruitment of nymphs from a direct hatch in July. Growth occurred through the summer months with most nymphs attaining maximum size before a winter quiescence. This assessment compared well with our limited data. Failure to collect adults was probably due to our infrequent sampling during their presumed early May emergence.

***Suwallia pallidula* and *Suwallia wardi*.** No aspects of the life histories of either *S. pallidula* or *S. wardi* have been reported. The latter was recently described from a Colorado Front Range springbrook (Kondratieff and Kirchner 1990). It was one of the most abundant chloroperlids in the Rio Conejos. This suggests that its ecological tolerance is wide and that it may soon be found in a variety of streams in the southern Rocky Mountains.

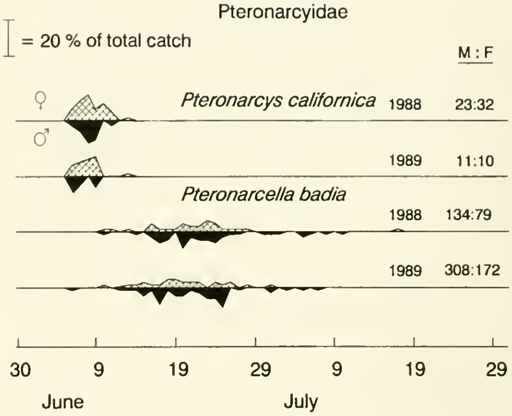

Fig. 15. Emergence of *Pteronarcella badia* and *Pteronarcys californica* from the Rio Conejos, 1988 and 1989. Polygons indicate daily relative proportion of total catch.

Several explanations are possible for the heavily female-skewed sex ratio (13 ♂:425 ♀) of *S. pallidula* adults. The most probable is a combination of limited use of emergence traps coupled with an inaccessible microhabitat of adult males, probably high in the vegetation. Parthenogenesis may also be possible, but it is exceedingly rare in stoneflies. Harper (1973a) reported that a few eggs of a perlid, *Paragnetina media* (Walker), hatched without fertilization. We did not attempt rearing of eggs from virgin females to check for parthenogenesis in either *Suwallia* spp. These sex ratios are a perplexing problem, compounded by the fact that 0 ♂: 657 ♀ of the closely related *S. lineosa* were caught during concurrent sampling on Massey Creek, a tributary of the Rio Conejos.

***Triznaka signata*.** Hassage and Stewart (1990) studied the widely distributed *T. signata* in the Rio Vallecitos of northern New Mexico. They reported a univoltine-slow growth pattern, with which we concur. No study of the emergence of this species has previously been published.

PERLIDAE

***Claassenia sabulosa*.** Hassage and Stewart (1990) and Barton (1980) report a merovoltine (>2 yr) growth pattern for New Mexico and Alberta populations of this species. No egg batches from the Rio Conejos hatched in our laboratory, but this Colorado population showed some evidence of an extended hatch leading to cohort splitting (Stewart and Stark 1988). Eggs may undergo a temperature-dependent quiescence as occurs in *Dinocras cephalotes* (Curtis) when fall temperatures decline to 8°C (Lillehammer et al. 1989). Presence of first-instar nymphs in the fall, eyed eggs in October and November, and more first-instar nymphs in March supported this contention.

Life histories have been reported for at least one species in every genus in the tribe Perlini, to which *C. sabulosa* belongs. All growth patterns involve 2–3 yr of development. *Agnetina flavescens* (Walsh), from an Ozark stream, exhibits a 2-yr life cycle, a short egg incubation period, and an extended emergence period

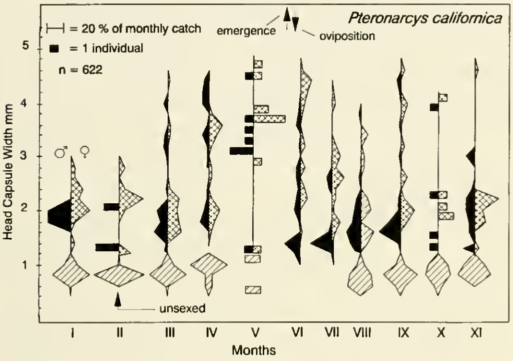

Fig. 16. Growth of *Pteronarcys californica* nymphs collected from the Rio Conejos, 1987–1990.

(Ernst and Stewart 1985b). *Agnetina capitata* (Pictet) was shown to have a 3-yr cycle, extended emergence, and a 40–80-d egg incubation period in Ontario (Harper 1973a). This range of incubation coupled with a long emergence promotes great differences in size of nymphs that ultimately prevents the separation of cohorts and determination of voltinism. This was also a problem for *C. sabulosa* in the Rio Conejos.

PERLODIDAE

This family contains over 115 species (Stark et al. 1986, Stewart and Stark 1988) in the Nearctic. Although life histories of only 26 species are known, a clear trend toward univoltine-slow cycles occurs among the subfamilies Isoperlinae and Perlodinae (Stewart and Stark 1988). Growth and emergence had not previously been studied for three of the seven perlodids in the Rio Conejos. These include *I. zionensis, I. quinquepunctata,* and *I. phalerata.*

Isogenoides zionensis. Few detailed life history studies of the genus have been reported (Stewart and Stark 1988). Barton (1980) supected semivoltinism for an Alberta population of *I. colubrinus,* since two size classes of nymphs were collected in early May. Flannagan (1977) reported great body length variation in May for this species in another Alberta watershed but concluded a univoltine-slow cycle. Hilsenhoff and Billmeyer (1973) and Dosdall and Lehmkuhl (1979) proposed univoltine growth patterns for the May–June-emerging *I. frontalis* in Wisconsin and Saskatchewan streams, respectively, based on samples taken a few months of the year. Semivoltinism, as reported for *I. zionensis* in the Rio Conejos, may also occur in its congeners, but this will be confirmed only when detailed studies using small mesh nets, frequent sampling, and egg rearing have been conducted.

***Isoperla* spp.** Of the three *Isoperla* whose partial growth patterns are presented here, only *I. fulva* has been previously reported. Hassage and Stewart (1990) reported a univoltine-slow cycle, with a June emergence in the Rio Vallecitos of New Mexico. We concur with the New Mexico study. Our results agree well with reviews of *Isoperla* biology, summarized for 12 Nearctic species through 1987 (Stewart and Stark 1988). Ten species were univoltine-slow, while only two were univoltine-fast.

In more recent literature Stewart et al. (1990) reported univoltine-slow growth for *I. petersoni* Needham & Christenson of Alaska. Additionally, Harper et al. (1994) added as univoltine-slow *I. francesca* Harper and *I. montana* (Banks) from Quebec populations. These and our Rio Conejos work bring to 17 the Nearctic *Isoperla* species known to exhibit univoltine-slow cycles, while only three species appear to be univoltine-fast. *Isoperla grammatica* (Poda) and *I. difformis* (Klapálek) (Malmqvist and Sjöström 1989) and *I. obscura* (Zetterstedt) studied by Ulfstrand (1968) are univoltine-slow in the Palearctic.

Up to seven species of *Isoperla* commonly occur in streams in North America (Stewart and Stark 1988); conversely, in Scandinavia rarely more than two species occur simultaneously (Malmqvist and Sjöström 1989). Congenerics of aquatic insects often partition resources along one or more resource gradients (Grant and Mackay 1969). Though only small numbers of adults were collected, a pattern of successive emergence of *I. fulva, I. quinquepunctata,* and *I. phalerata* was clear in the Rio Conejos. Fifty percent cumulative catch dates for *I. fulva, I. phalerata,* and *I. quinquepunctata* were 22 June, 28 June, and 14 July, respectively, for 1988. These dates for 1989 were 18 June, 25 June, and 5 July. Temporal segregation brought about by a gradual change in dominance (Illies 1952) of these species may have accounted for the pres-ent coexistence of these stoneflies.

Skwala americana. Two other studies reported univoltine-slow cycles with emergence from February through April for this species in northern New Mexico and central Colorado (Short and Ward 1980, Hassage and Stewart

1990). *Skwala curvata* (Hanson) of California also exhibited a univoltine-slow cycle, with emergence in April and May (Sheldon 1972). Other Arcynopterygini with univoltine-slow growth include *Frisonia picticeps* (Hanson) in California (Sheldon 1972), *Megarcys signata* (Hagen) in Utah (Cather and Gaufin 1975), and *Perlinodes aurea* (Smith) in California and Alberta (Radford and Hartland-Rowe 1971, Sheldon 1972).

Sheldon (1972) estimated average total fecundity of *S. curvata* to be near 1780 eggs for preemergent nymphs. This is much greater than that proposed for *S. americana* from the Rio Conejos. He used interocular width as an index to predict fecundity. Conversion of interocular width to HCW likely involves a factor of 2X, which would make *S. curvata* the larger of the two stoneflies. This largely accounts for differences in fecundity. Mutch and Pritchard (1986) reported that *S. americana* (as *S. parallela*) had a warm, stenothermal egg development.

Most species in this family have conserved the life history traits that Lillehammer et al. (1989) proposed as ancestral. These traits include univoltine-slow cycles, temperature-dependent growth, and direct egg development. *Isoperla quinquepunctata* and *I. zionensis* have likely abandoned all of these except temperature-dependent growth.

PTERONARCYIDAE

Pteronarcella badia. Gaufin et al. (1972) reported that a 2-yr life cycle was possible for this species in Utah; however, S. Perry et al. (1987) and Stanford (1975) reported a univoltine life history in Montana. No eggs were reared in either Montana study, and it is apparent from their growth histograms that early instars were missed entirely. Therefore, semivoltine life history is most probable throughout its range.

Nymphs of this species are more likely to be found aggregated on filter paper leaf models than alone (Hassage et al. 1988). We have also observed nymphs aggregating under margin cobble immediately before emergence. Adults aggregate in leaf debris at the base of willow and cottonwood coppices at the Rio Conejos. This behavior may be attributable to the transformation and nighttime refuge sites being contagiously distributed. Hassage et al. (1988) also postulated that aggregation in *P. badia* lowers individual risk to predation.

Pteronarcys californica. The egg diapause plus 38-mo nymphal life span places total life span of this population at 4 yr. This is one of the longest-lived aquatic insects known to occur in the Nearctic. Additionally, this species is perhaps our most synchronously emerging stonefly.

Two- to 3-yr life cycles with a 9–10-mo egg diapause occur in other *Pteronarcys* such as *P. dorsata* (Barton 1980), *P. proteus* (Holdsworth 1941a, 1941b, W. Perry et al. 1987), and *P. scotti* in the southern Appalachian Mountains (Folsom and Manuel 1983). However, Lechleitner and Kondratieff (1983) detailed a 1-yr life history for *P. dorsata* in Virginia.

Multiple-year life histories are common among larger species of the Pteronarcyidae (Stewart and Stark 1988). Accompanying this long nymphal growth, and perhaps contributing to it, is another life history trait, long egg diapause. Univoltine growth patterns and direct egg development are ancestral patterns, while the semivoltine growth and diapause of *P. badia* and *P. californica* are derived traits (Lillehammer et al. 1989). Future studies of egg incubation in lower latitudes of North America will enable us to outline the range of responses of which *Pteronarcys* and *Pteronarcella* are capable.

Unanswered Questions

Several largely unanswered questions persist about the life histories of stoneflies in and along the Rio Conejos. We have found that nymphs of many chloroperlids are not available in surface sediments until just prior to emergence. They must be hyporheic in their habitat choice. Second, chloroperlids of the present study did not readily produce eggs in captivity, and those incubated never hatched. We can still ask many questions about their life histories. The answers would require a detailed study of the hyporheic habitat of an open-sediment stream like the Rio Conejos. This study should concentrate only on the chloroperlids, since they are generally abundant and diverse. Such a study would still fit within the comparative study approach of Sheldon (1972), but the guild would involve hyporheic chloroperlids.

To settle the dilemma of aberrant sex ratios in this family, studies must concentrate on the presence of male nymphs in the stream. In this way the search for adult males whose whereabouts are unknown need not take place, since both sexes of nymphs presumably enjoy a similar microhabitat. If no male nymphs are located, then incubation of eggs from virgin females should be conducted to confirm the possibility of parthenogenesis.

An exciting observation we made during the study was that of basking in the sun of nearly all adults of summer-emerging species. Most displayed a remarkably consistent pattern of ascendence of riparian vegetation beginning at about 0800 h. Activity usually ceased by 1300 h when air temperatures were hottest. This ascendence culminated for females in egg batching and oviposition flights, while males used these riparian staging grounds for mate searching, drumming, and mating. Stoneflies should be investigated for potential to benefit from basking, an unreported phenomenon for Plecoptera.

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POLLINATOR SHARING BY THREE SYMPATRIC MILKVETCHES, INCLUDING THE ENDANGERED SPECIES *ASTRAGALUS MONTII*

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ABSTRACT.—Insects visiting flowers of the endangered Heliotrope milkvetch, *Astragalus montii,* were compared with those visiting two common sympatric congeners, *A. kentrophyta* and *A. miser,* on three sites on the Wasatch Plateau of central Utah for 2 yr. We recorded 27+ species of bees, most of which were uncommon, visiting the three species. All three species were primarily visited by native bees of the genera *Osmia* (15 species) and/or *Bombus* (4 species). Most *Osmia* species visited the three species of *Astragalus* indiscriminantly; bumblebees preferred *A. miser* and avoided *A. montii.* Our hypothesis that *A. montii* flowers would receive fewer total bee visits and be visited by fewer bee species than their common congeners was rejected: *A. montii* was intermediate to the two common species in its attractiveness to bees. Also rejected was our hypothesis that the greater similarity between *A. montii* and *A. kentrophyta* in flower size, flower morphology, and microhabitat would be associated with greater similarity of flower visitors than either had with *A. miser.* The data suggest that, rather than competing with each other for pollinators, the three species of *Astragalus* facilitate each other's visitation rates.

Key words: Astragalus, *milkvetch, endangered plant, reproduction, pollination, facilitation, bee diversity, conservation, Fabaceae,* Osmia.

Many insects such as dipterans and lepidopterans use flowers only as fuel stations (Elton 1966); they collect nectar and burn it as they search for suitable spots to lay eggs. Such insects may merely pass through areas where flowers are sparse. Bees, in contrast, are central-place foragers (Orians and Pearson 1979) that must consistently reap profits in both nectar and pollen, for they forage not simply to underwrite their own movements, but to provide food to rear their progeny as well (Stephen et al. 1969). Because bees are under strong, selective pressure to be profitable foragers, they are attracted to dense patches of flowers (Heinrich 1976, 1979, Thomson 1982). Bumblebees, for example, quickly recognize and exploit particularly rewarding flower patches (Heinrich 1976, 1979); other bees probably do so also.

Density-dependent foraging behavior by bees has important implications for certain rare plants. Rabinowitz (1981) distinguished seven types of rarity in plants using the following three criteria: (1) local abundance, (2) habitat specificity (narrow or wide), and (3) geographic range (large or small). Those species with both narrow habitat specificity and small local populations (regardless of geographic range) are sparse and likely to attract foraging bees only incidentally. We expect such species to be pollinator-vulnerable and, therefore, to be highly self-compatible and perhaps primarily self-pollinating (Karron 1987). It is less clear whether plants in other categories of rarity, especially endemics (Rabinowitz 1981, Kruckberg and Rabinowitz 1985), are also pollinator-vulnerable. Endemics have narrow habitat specificity but may be locally abundant.

One such endemic, the rare Heliotrope milkvetch, *Astragalus montii* Welsh, is limited to a few isolated populations in limestone gravel outcrops on the Wasatch Plateau of central Utah at about 3350 m. There it grows with two common congeners, *A. kentrophyta* var. *tegetarius* (S. Wats.) Dorn, hereafter *A. kentrophyta,* and *A. miser* var. *oblongifolius* (Rydb.) Cron., hereafter *A. miser.* In all three species, seed production requires, or is increased by, pollinator visits to flowers (Geer and Tepedino 1993). Information on the identity and biology of these pollinators is important, for *A. montii* occurs on rangelands that are grazed by domestic livestock and sprayed with insecticides to control grasshoppers. Successful management of this rare species requires knowledge of how such spraying may affect its pollinators.

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In this report we compared composition and abundance of pollinator fauna of *A. montii* with those of its two sympatric congeners. Because there may be wide variation in a species' pollinators between years and sites (Tepedino and Stanton 1981, Herrera 1990, Eckhart 1992), we censused pollinators of *A. montii* and its congeners for 2 yr at three sites. We hypothesized that *A. montii* would (1) attract fewer individual pollinators, (2) have lower pollinator species diversity than its two common congeners, and (3) share more species of flower visitors with *A. kentrophyta* than with *A. miser* because similarity in plant and flower size, flowering time, and microhabitat is greater with the former than with the latter.

SPECIES AND STUDY AREAS

All three species of *Astragalus* are small perennial herbaceous legumes. *A. montii* is restricted to three mountaintops on the Wasatch Plateau in central Utah. Although Isely (1983) proposed that *A. montii* be reduced in status to a variety of *A. limnocharis* Barneby, it was listed as endangered under the Endangered Species Act in 1987 as *A. montii* and remains so (Anonymous 1991). Therefore, we refer to this taxon as *A. montii*.

A. kentrophyta and *A. miser* are widespread species that occur with *A. montii* at three sites on two of the mountains; the third mountain is less accessible and was not included in the study. *A. kentrophyta* is widespread and abundant in the Rocky Mountains, mostly between 2280 and 3650 m. *A. miser*, one of the most common species of *Astragalus* in the Rocky Mountains, is locally abundant from sagebrush foothills to the spruce-fir belt (Barneby 1989). The three species co-occur at 3250 to 3350 m in an Engelmann spruce (*Picea engelmannii* Parry)/subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) community. *A. montii* and *A. kentrophyta* are intermingled in limestone gravel outcroppings where *A. miser* is found only occasionally. *A. miser* is most abundant nearby where soil is deeper and less rocky. *A. montii* and *A. miser* occur at similar local densities on Heliotrope Mountain (9.3 ± 0.1/m^2 and 12.6 ± 8.3/m^2; Geer unpublished data). There are fewer *A. kentrophyta* (2.6 ± 0.8/m^2; Geer unpublished), but individuals cover more ground than do those of its congeners. The three species overlap in bloom time for about 3 wk (Fig. 1).

Heliotrope milkvetch is a subacaulescent plant 1–5 cm tall that arises from a branched caudex. Flowers are deep purple with white wingtips. There may be a dozen to a hundred or more flowers (7.8 ± 1.5 mm long, N = 10; Geer unpublished) per plant, two to eight per raceme (Barneby 1989). It does not appear to reproduce vegetatively (personal observation). In 1989 and 1990 *A. montii* commenced flowering with final snowmelt beginning as early as June and continuing for about 4 wk until mid-July (Fig. 1).

The common species *A. kentrophyta* started to flower approximately 1 wk before *A. montii* and continued to flower through early August. It is prostrate, with stems that fork repeatedly and closely to form low convex cushions covered with small blue-white to purplish flowers (6.6 ± 1.2 mm long, N = 10; Geer unpublished), only two per raceme (Barneby 1989).

The other common congener, *A. miser*, commenced flowering 1–2 wk after *A. montii* and continued flowering until September. It is taller (2–20 cm) than *A. montii* or *A. kentrophyta*. Flowers are larger (11.4 ± 1.4 mm long, N = 11; Geer unpublished) and vary in number per raceme (3–15; Barneby 1989) and in color; flowers may be white, pink, or lavender.

All *Astragalus* species have papilionaceous blossoms composed of a showy standard or banner petal, a keel that protects the joined stamens and pistil, and two wings that, along with the keel, typically serve as a landing platform (Kalin Arroyo 1981). To trip *A. miser* flowers, bees land on the keel and force their way under the banner (personal observation) as they do for other species of *Astragalus* (Green and Bohart 1975, Faegri and van der Pijl 1979). Visitors to *A. montii* or *A. kentrophyta* spread the wing petals with their midlegs and take nectar, or comb pollen from the anthers to their abdominal pollen baskets with their forelegs (personal observation). Stylar hairs (termed a brush mechanism) aid in the collection of pollen by transporting it from the keel outward (Kalin Arroyo 1981).

Sexual reproduction by *A. miser* and *A. kentrophyta* requires insects to transfer pollen; *A. montii* is capable of unassisted self-pollination (autogamy). However, fruits produced autogamously by *A. montii* may be inferior in

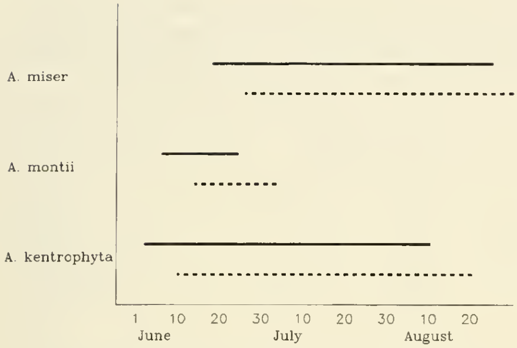

Fig. 1. Blooming dates for three co-occurring species of *Astragalus* at the SSH site. Solid line = 1989; dashed line = 1990.

quality to those produced by geitonogamous or xenogamous hand pollinations, or open-pollinated control treatments (there are fewer seeds per fruit and seeds are smaller; Geer and Tepedino 1993). Thus all three species probably benefit from insect visitation.

METHODS

Insect visitors were collected for about 3 wk in 1989 and for 2 wk in 1990 at the following three sites, starting when *A. montii* was in peak bloom: the head of Mill Stream on Ferron Mountain (HMS), south side of Heliotrope Mountain (SSH), and east end of Heliotrope Mountain (EEH). In 1990 collections from all three *Astragalus* species were made only at the SSH site because only two insect collectors were available instead of four, as in 1989. We concentrated on the SSH site in 1990 to make the number of collector hours there equivalent to the 1989 effort. In 1990 visitors to *A. kentrophyta* were collected at the SSH and HMS sites, and visitors to *A. miser* were collected at the SSH and EEH sites. Following are approximate direct distances between sites: HMS to SSH = 3.6 km, HMS to EEH = 2.4 km, and EEH to SSH = 1.2 km.

Pollinators were collected with a standard butterfly net and killed in cyanide jars. Cold temperatures, strong winds, and frequent precipitation (snow and rain) prohibited pollinators from flying during all but brief windows of calm, sunny weather, so opportunistic collection was necessary to ensure an adequate sample size. Collections were made from all three species contemporaneously, whenever weather permitted (i.e., temperatures $>13°$C, little wind, and no precipitation). Initially, sight identification of some taxa was attempted so as to reduce impact on the pollinator community. It soon became obvious that it was impossible to identify *Osmia* and other individuals without laboratory examination. Subsequently, all flower visitors were collected whenever possible. Few insects other than bees visited the flowers.

Diversity of bee visitors to each *Astragalus* species was calculated using Simpson's diversity index, $D = 1 - \Sigma^{s}_{i=1} (P_i)^2$, where P_i = the proportion of individuals that belong to each bee species (Southwood 1978). Simpson's index gives little weight to rare species and more weight to common ones. Similarity of the bee fauna visiting *Astragalus* species was estimated using Czekanowski's similarity index: $C_s = NJ/(a+b+...n)$, where N is the number of plant species being compared, J is the number of bee species shared by those plant species, and a, b, etc., are the total number of bee species visiting each plant species (Southwood 1978). C_s is based on species presence alone. We also calculated C_j, which adjusts for the number of individuals per species (Southwood 1978). The indices range from 0 (no similarity) to 1.0 (complete similarity). They were calculated between pairs of species and among all three species.

Probable pollinators of the three *Astragalus* species were ascertained by examining flower visitors and recording areas of their bodies on which pollen was found. Specimens were then relaxed and pollen was removed using an insect pin or by dabbing it with acid-fuchsin gel (Beattie 1971). The pollen was placed on a glass slide with acid-fuchsin gel, warmed until liquid, and a cover slip applied (modified from Faegri and Iverson 1964). One slide per leg or two slides per abdomen were made for each insect. All slides were viewed at 100X magnification and the pollen compared to a pollen reference collection of species in bloom at the study sites.

RESULTS

Bees were scarce at the study sites in both years (Table 1, Appendices I, II). Bee visitors per plant species ranged from about 0.5 to just over 3 per hour, a small number considering that many flowers of each species were being monitored. Bee numbers were higher in 1990;

TABLE 1. Number of person hours spent collecting and number of bee individuals collected or observed visiting flowers of *Astragalus montii* (Asmo), *A. kentrophyta* (Aske), and *A. miser* (Asmi) at three sites on the Wasatch Plateau in 1989 and 1990. SSH, EEH = south and east side Heliotrope Mountain, respectively; HMS = head of Mill Stream, Ferron Mountain.

	SSH			EEH			HMS		
	Asmo	Aske	Asmi	Asmo	Aske	Asmi	Asmo	Aske	Asmi
1989									
Hours	24	8	10	30	24	22	8	16	16
Individuals	28	9	10	30	19	10	5	11	18
Individuals/hour	1.2	1.1	1.0	1.0	0.8	0.5	0.6	0.7	1.1
Species	7	3	5	7	7	3	3	4	7
1990									
Hours	30	15	15	12	12	—	12	—	12
Individuals	57	7	35	40	24	—	16	—	24
Individuals/hour	1.9	0.5	2.3	3.3	2.0	—	1.3	—	2.0
Species	10	5	11	5	5	—	6	—	3

when categorized by site and *Astragalus* species visited, six of seven categories had more individuals per hour in 1990 than in 1989.

The initial hypothesis, that *A. montii* would have fewer individual flower visitors than would its common congeners, received little support (Table 1, Appendices I, II). In 1989 there was little difference among species in visitors per person hour at SSH. At EEH *A. montii* flowers were visited more often than the other species. Conversely, at HMS *A. montii* flowers received the fewest visits. In 1990 comparisons of number of visitors among all three *Astragalus* species could be made only at the SSH site where *A. montii* had an intermediate number of visitors per hour. At EEH, *A. montii* again had more visits per hour than *A. kentrophyta*, and at HMS it had fewer visits per hour than *A. miser*.

The prediction that species richness and species diversity of bees visiting the three *Astragalus* species would be lowest for *A. montii* was also provisionally rejected. The number of species captured on *A. montii* commonly exceeded those captured on the other species, both when more hours were spent collecting from *A. montii* than the other species (1989 SSH) and when collecting hours were equal (1990 HMS; Table 1). Only once, when fewer hours were spent collecting on *A. montii* than on the other *Astragalus* species (1989 HMS), was *A. montii* visited by the fewest species of bees. When all sites were considered, total number of species collected on *A. montii* in 1989 exceeded those captured on *A. kentrophyta* and equaled those captured on *A. miser* (Table 2). In 1990 more species were caught visiting *A. montii* than the other two species, but this difference is probably because we collected at three sites for *A. montii* but at only two for each of the other two species.

Calculations using species diversity, D′, also failed to yield expected trends (Table 2). In 1989 diversity of visitors to flowers of *A. montii* was very similar to diversity recorded for *A. kentrophyta* and *A. miser*. Comparisons for 1990 are more tenuous because of the differences among species in number of sites sampled. However, diversity of flower visitors was highest for *A. miser* and similar for *A. montii* and *A. kentrophyta*. Diversity in 1990 was generally lower than in 1989, although number of individuals captured was greater.

The most frequent visitors to these *Astragalus* species in both 1989 and 1990 were *Osmia* bees (Table 3). For the small-flowered *A. montii* and *A. kentrophyta*, in both years >70.0% of all visitors were *Osmia* bees. Only for *A. miser* in 1990 did the percent *Osmia* visitors drop below 50%. *A. miser* was more frequently visited by bumblebees, especially at SSH. The abundance of bumblebees caused SSH to have the lowest percentage of *Osmia* individuals recorded at any site in both years. Even so, *Osmia* bees were always more than 60% of the total flower visitor fauna recorded in any site-year.

Because of greater similarities in flower size, color, and microclimate, we expected *A. montii* and *A. kentrophyta* to have more visitors in common than either did with *A. miser*. This was not true in either year. The three pairings of *Astragalus* did not differ much in the number of bee species they shared, though results

TABLE 2. Number of individuals, number of species, and species diversity (D) of bees found visiting three species of *Astragalus* at three sites on the Wasatch Plateau. In 1989 collections were made for each species at all three sites; in 1990 collections were made at all sites for *A. montii*, but at only two sites for the other two species. For comparative purposes, collection data for the latter two species are shown in 1989 for all three sites and for only the two sites collected at in 1990. D = Simpson's diversity index.

Astragalus species	Individuals		Species		D[1]	
	3 sites	2 sites	3 sites	2 sites	3 sites	2 sites
1989						
montii	63	—	13	—	0.87	—
kentrophyta	39	28	9	8	0.79	0.81
miser	38	28	13	11	0.88	0.87
1990						
montii	113	—	13	—	0.62	—
kentrophyta	—	31	—	7	—	0.60
miser	—	59	—	12	—	0.79

[1] In 1989 only indiviuals that were collected were used in calculations, because uncaptured *Osmia* individuals were not identifiable to species.

TABLE 3. Percent visitors that were *Osmia* bees to the flowers of three *Astragalus* species (abbreviations as in Table 1). Data shown grouped by species across sites, and by site across species, for 2 yr. For comparative purposes, 1989 data are shown in entirety (3 sites or 3 species) or only for the 2 sites or 2 species sampled in 1990.

	Asmo	Aske	Asmi	SSH	EEH	HMS
	Across sites			Across species		
1989						
3 (sites/species)	88.9	71.8	73.7	62.3	88.1	76.5
2 (sites/species)	—	78.6	64.3	—	85.7	87.0
1990	93.8	74.2	47.5	62.6	87.5	95.0

varied somewhat with year and with index used (Table 4). In 1989 the three pairings of *Astragalus* species had about the same number of bee species in common. In 1990 *A. miser* and *A. montii* had about twice the number of species in common as did the other pairings. Neither coefficient of similarity, C_s or C_i, consistently supported the hypothesis; in 1989, but not 1990, C_s and C_i were highest for the *A. montii–A. kentrophyta* comparison.

Many bees visiting *Astragalus* flowers carried pollen on their bodies: 43% of the bees captured, primarily females of the genus *Osmia*, had been collecting pollen. Pollen loads comprised primarily *Astragalus* pollen (all means >80%; Table 5). It is unknown whether loads commonly contained more than one species of *Astragalus* because pollen grains could not be distinguished to species with the light microscope.

Our observations of foraging bees suggest some interspecific movement. In 1989 few *Osmia* individuals flew between *A. montii* and *A. miser* or *A. kentrophyta*; of 74 interplant movements only two were interspecific. In 1990, 4 of 21 observed interplant movements were between species. Interspecific visits occurred most commonly where species grew intermingled.

DISCUSSION

Two hypotheses make predictions about the abundance and diversity of visitors to the flowers of rare plants. For entomophilous plants, Levin and Anderson (1970), Straw (1972), and Karron (1987) proposed that pollinators should be more flower constant to abundant plant species than to rare ones, that this differential flower constancy would result in more successful reproduction by "majority" species than by "minority" species, and that over time minority species would become extinct because of dwindling recruitment or would evolve some method of self-reproduction (Levin 1972). A corollary of this hypothesis is that both the number and diversity of visitors to the flowers of rare plants should be lower than they are to abundant ones.

TABLE 4. Number of bee species (S) collected on each *Astragalus* species, and number of species shared (C) and similarity indices for each pairing for each year. C_s = Czekanowski's similarity index for bee species presence-absence; C_i = index weighted by individuals captured.

Astragalus species pair	1989 S	1989 C	1989 C_s	1989 C_i	1990 S	1990 C	1990 C_s	1990 C_i
montii	13	6	0.50	0.34	13	7	0.56	0.37
miser	13				12			
montii	13	6	0.55	0.43	13	4	0.40	0.35
kentrophyta	9				7			
kentrophyta	13	5	0.45	0.43	12	3	0.32	0.53
miser	9				7			
All three species	20	4	0.35	0.27	21	3	0.28	0.30

In contrast, the facilitation hypothesis (reviewed by Rathcke 1983) predicts that rare species growing with attractive, more abundant species may actually reproduce more successfully because the latter draw many more pollinating insects into the area than would otherwise be present. If so, rare and abundant sympatric species should have similar visitor diversity, and visitor abundances should reflect respective frequencies of the plants. This study indirectly assessed the importance of facilitation and competition. A direct assessment is difficult because (1) the experiments necessary to distinguish between alternatives cannot be conducted when the "plant protagonist" is protected by the Endangered Species Act; and (2) *A. montii* did not occur in the absence of its congeners on our study sites, so visitation rates of "facilitated" and "unfacilitated" populations could not be compared.

Our results supply consistent, though indirect, support for the facilitation hypothesis. Except for bumblebees, which foraged almost exclusively from large-flowered *A. miser*, bees did not discriminate against *A. montii* but rather seemed to treat all three *Astragalus* species as one taxa. First, *A. montii* did not consistently attract fewer visitors per hour than did the other species. Indeed, visitation rates to *A. montii* were higher than to the other species in three of six site-years (Table 1). Second, neither species richness nor species diversity of pollinators was consistently lower for *A. montii* than for the other species (Table 2). In fact, an equal or greater number of species visited *A. montii* than visited the others in both years. And finally, bees were observed moving between species on individual foraging trips. Gross (1992) also reported that bees foraging on closely related legumes commonly moved between species. Thus, there was no detectable rare species disadvantage and no evidence that endemics, at least those growing in close proximity to abundant congeners, are pollinator-vulnerable.

The shared microhabitat and similarities in flower size and morphology of *A. montii* and *A. kentrophyta* led us to expect that facilitation would be more likely between these two species and, therefore, that they would have more visitors in common than either would with *A. miser*. For example, Thomson (1978, 1981, 1982) found that, in two-species mixtures, the degree of intermingling and the similarity in structure and appearance of congeners' flowers determined the importance of competition and mutualism. The more similar the flowers, the more likely that visitation rates to rare species would be bolstered by the presence of abundant species and the more likely that visitors would be shared. Our data supported this expectation for 1989 but not for 1990 (Table 4). In 1990 C_s for the *A. montii–A. kentrophyta* comparison was intermediate to the other comparisons; for C_i it was lower than the other comparisons. Thus, results for the similarity analyses also tend to support the hypothesis that most bees do not distinguish among these *Astragalus* species when foraging, and that the *Astragalus* species tend to facilitate each other's visitation rates.

Only bumblebees seem uninfluenced by *Astragalus* flowers in the aggregate. They clearly preferred flowers of *A. miser* and avoided those of the other *Astragalus* species. Flowers of *A. miser* are large, probably more rewarding, and provide a landing platform from

TABLE 5. Percent *Astragalus* pollen grains in pollen loads, and location of pollen loads carried by bees collected on three *Astragalus* species at three sites on the Wasatch Plateau in 1989 and 1990.

Astragalus species	Number of pollen loads	Mean % *Astragalus* pollen (+SE)	Location of pollen	
			Abdomen	Legs
montii	45	82 ± 4	42	3
miser	19	90 ± 1	19	—
kentrophyta	5	95 ± 1	5	—

which large, energy-demanding bumblebees can readily forage. Other large-flowered *Astragalus* species also attract numerous large bees such as bumblebees (*Bombus* spp.) and anthophorids (Green and Bohart 1975, Sugden 1985, Karron 1987). In comparison, bumblebees seemed unable to land on the small, weakly supported *A. montii* flowers which are borne above the foliage; they did occasionally exploit the tiny *A. kentrophyta* blossoms while perched on the foliage of that cushion plant.

Factors other than flower abundance can influence the flight path of foraging bees. Because bees are central-place foragers (Orians and Pearson 1979), travel time and energy expended between flower patches and nest are also important. Thus, bees may patronize a flower patch because of its proximity to their nest, even though flowers are more abundant elsewhere. For example, *Osmia* bees mated and nested at the sheltered EEH site where relatively few *A. kentrophyta* or *A. miser* plants grew; the population of *A. montii* was small but dense. Nevertheless, bees visited flowers at least as frequently at EEH as at the other, more flower-rich, sites (Tables 1, 2). Thus, suitability of nesting habitat at EEH, rather than *Astragalus* flower abundance, may best account for the abundance of bees there. The effect of wild bee nesting sites on seed production of surrounding vegetation is poorly studied and warrants additional attention.

Rigorous subalpine communities of the Wasatch Plateau, with frequent high winds, thunderstorms, and below-freezing temperatures during the blooming season, support a surprisingly rich bee fauna. In 2 yr we collected 27+ bee species foraging on *Astragalus* flowers during 2–3 wk (Appendices I, II). These bees are invaluable pollinators of native plants both rare and common. Their welfare must also be considered in management plans for rare plants. Land managers must eliminate losses of bees to insecticide applications made for rangeland grasshoppers and minimize physical damage to nest sites. The present insecticide-free buffer zone (currently 4.8 km) around rare plant populations should continue to be maintained. Areas where bees nest in soil should also be protected from livestock trampling, off-road vehicle use, and foot traffic (Sugden 1985). Such diversity, comparable to or greater than that of other subalpine areas in North America (Moldenke and Lincoln 1979), is to be marveled at and preserved.

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APPENDIX I. Species of bees collected and observed visiting flowers of *A. montii* (Asmo), *A. miser* (Asmi), or *A. kentrophyta* (Aske) at three sites in 1989. Entries represent number of males/females collected. Observations are in parentheses. Site abbreviations as in Table 1.

	SSH 1–21 June			EEH 14–25 June			HMS 14–22 June		
Bee species	Asmo	Aske	Asmi	Asmo	Aske	Asmi	Asmo	Aske	Asmi
ANDRENIDAE									
Andrena transnigra Vier.	0/1								
Andrena spp.					(1)				

APPENDIX I. Continued.

	SSH 1–21 June			EEH 14–25 June			HMS 14–22 June		
Bee species	Asmo	Aske	Asmi	Asmo	Aske	Asmi	Asmo	Aske	Asmi
APIDAE									
Bombus bifarius Cr.			0/1						
Bombus flavifrons Cr.			(0/2)						
Bombus huntii Greene			(0/2)						0/2
Bombus nevadensis Cr.			0/1						
HALICTIDAE									
Evylaeus niger (Viereck)	0/1								0/1
MEGACHILIDAE									
Anthidium tenuiflorae Ckll.	(2)1/0			(1)	(1)1/2(1)			1/2(2)	
Megachile spp.	(1/0)		(1/0)						
Osmia cyanopoda Ckll.		1/0							
Osmia hurdii White	0/1								
Osmia longula Cr.									0/1
Osmia nigrifrons Cr.		0/1		0/4	0/2				0/3
Osmia aff. *nigrifrons*	0/3						0/1	0/1	
Osmia paradisica Sanh.				1/0					2/2
Osmia penstemonis Ckll.				0/1					
Osmia pikei Ckll.							0/1		
Osmia pusilla Cr.					0/1				1/0
Osmia sladeni Sanh.		2/0		1/0	4/0	3/0		2/0	
Osmia sladeni &/or *alpestris*				0/2	0/3	0/2	0/1	0/2	0/5
Osmia tanneri Sanh.	1/3			1/2	0/1	0/1			
Osmia spp.	(5/9)	(1/4)	(0/3)	(8/9)	(1/1)	(1/3)	(1/1)	(0/1)	(0/1)

APPENDIX II. Species of bees collected and observed visiting flowers of *A. montii* (Asmo) at three sites and *A. miser* (Asmi) and *A. kentrophyta* (Aske) at two sites each in 1990. Entries represent number of males/females collected. Observations are in parentheses. Site abbreviations as in Table 1.

	SSH 19 June–4 July			EEH 19–29 June		HMS 21–29 June	
Visitor	Asmo	Aske	Asmi	Asmo	Aske	Asmo	Asmi
ANDRENIDAE							
Andrena nigrihirta (Ashm)			0/1				
Andrena transnigra Vier.	0/1						
APIDAE							
Apis mellifera L.			0/1(5)				
Bombus bifarius Cr.			0/1				
Bombus flavifrons Cr.	0/1	0/1					
Bombus huntii Greene			0/3(6)				
Bombus nevadensis Cr.			0/3(5)				
MEGACHILIDAE							
Anthidium tenuiflorae Ckll.	1/0(2)		2/0		0/1(3)		
Hoplitis fulgida Cr.					3/0		
Megacile melanophaea Smith			2/0			1/0	1/0
Megachile perihirta Ckll.	1/0		1/0				

APPENDIX II. Continued.

	SSH 19 June–4 July			EEH 19–29 June		HMS 21–29 June	
Visitor	Asmo	Aske	Asmi	Asmo	Aske	Asmo	Asmi
MEGACHILIDAE (continued)							
Osmia longula Cr.				2/0			
Osmia montana Cr.					1/0		
Osmia aff. *nigrifrons*	0/1		0/1				
Osmia paradisica Sanh.	1/0		0/2	3/0		1/2	1/0
Osmia penstemonis Ckll.						0/1	
Osmia pusilla Cr.		0/1					
Osmia sculleni Ckll.	2/0			1/0			
Osmia sladeni Sanh	19/13	4/0	1/0	8/16	7/8	3/6	1/21
Osmia subaustralis Ckll.	4/0					1/0	
Osmia tanneri Sanh.	9/2	1/0	1/0	9/1	1/0	0/1	

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FACTORS AFFECTING SELECTION OF WINTER FOOD AND ROOSTING RESOURCES BY PORCUPINES IN UTAH

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ABSTRACT.—Ecological and phytochemical factors potentially affecting winter dietary discrimination by porcupines (*Erethizon dorsatum*) in the mountain brush zone of Utah were studied. Porcupines utilized gambel oak (*Quercus gambelii*) as their primary winter food and roosting resource. Big-tooth maple (*Acer grandidentatum*) was the most common tree species in the study area but was rarely utilized by porcupines. Conifer species were used as a food and roosting resource significantly less often than they occurred in the study area, despite thermal advantages provided by their relatively dense canopies. Oak feed trees were successfully separated from conifer feed trees by discriminant analysis 100% of the time. Oak trees were correctly classified as feed and nonfeed trees 71% of the time. Gambel oak contained higher amounts of crude protein, fiber, and tannins, but was lower in ether extract fractions and fatty acid content than conifers. A layer of adipose tissue used as an energy reserve by porcupines may have relaxed energy intake demands sufficiently to permit them to concentrate on a diet of oak tissue, which is high in protein, rather than a high-fat conifer diet. A diet relatively high in protein may have facilitated digestion of food material high in fiber. Temperature did not affect selection of tree species used for roosting. Rock and snow caves were utilized infrequently and the study population ranged widely. Three of 15 study animals were eaten by predators.

Key words: porcupine, Erethizon dorsatum, *gambel oak,* Quercus gambelii, *dietary selection, mountain brush zone, predation.*

Porcupines (*Erethizon dorsatum*) roost and feed in canopies of deciduous trees and shrubs for extended periods during winter in much of western North America (Oveson 1983, Craig and Keller 1986, Sweitzer and Berger 1992). Apparent localized interspecific and intraspecific preferences for food and shelter resources by porcupines imply that chemical and/or physical advantages are available to them. Further, since snow caves, rock dens, and cover in canopies of coniferous tree species likely offer increased thermal advantages in the form of energy savings to porcupines (Clarke and Brander 1973, Roze 1987, 1989), their dependence on a deciduous food and roosting resource (which does not offer those advantages) further strengthens the implication that chemical and/or physical selective advantages are realized by dietary selection. Predator avoidance may also be an important force in food and roost tree selection. The objective of this research was to investigate physical, phytochemical, and ecological agents involved in selection of gambel oak by porcupines in south central Utah.

STUDY AREA

The study was conducted in the mountain brush zone near the mouth of Spanish Fork Canyon in north central Utah. Elevations at the study site range from 1650 to 2075 m. The general exposure is northern, and terrain is steep. Overstory woody vegetation is dominated by gambel oak (*Quercus gambelii*) and bigtooth maple (*Acer grandidentatum*). Aspen (*Populus tremuloides*), chokecherry (*Prunus virginiana*), Douglas fir (*Pseudostuga menziesii*), white fir (*Abies concolor*), and mountain maple (*Acer glabrum*) are also represented in the woody flora. The climate in Spanish Fork Canyon during the winter of 1984–85 was not atypical. Data from the Spanish Fork U.S. Climatological Station, located approximately 5.5 km from the study site, indicate that temperatures were slightly colder and precipitation was slightly higher than average (U.S. Climatological Data for Utah 1984–85). Coyote (*Canis latrans*) and mountain lion (*Felis concolor*) tracks were frequently encountered in the study area. Private access into the study area allowed observation of a porcupine population relatively free from human disturbance.

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METHODS

Fieldwork

We conducted fieldwork from late December 1984 through April 1985, at which time the study population had shifted from a diet of inner bark (phloem and cambium) of woody vegetation to herbaceous vegetation. The study area was systematically searched by researchers on snowshoes. Study animals were captured by hand, usually while they were still in tree canopies. This was accomplished by grasping distal guard hairs at the posterior end of the tail between thumb and forefinger and pulling the tail taut. The captured animal was then secured by grasping the tail with the free hand using a backward stroking motion to flatten the quills. Fifteen porcupines, 10 females and 5 males, were instrumented with radio transmitter collars (Telonics, Inc.). Animals were located daily by triangulation, and visual sightings were made on each animal approximately weekly.

Percent occurrence of woody species was calculated from point-quarter measurements using the feed/roost tree as the center point (Cottam and Curtis 1956). Percent occurrence of woody species vs. percent utilization of each feed tree species was compared using chi-square analysis to test whether feed tree selection was random. Diameter at breast height (dbh), species, and distance from the feed tree center point were recorded for the nearest woody stem in each quadrant. Point-quarter measurements were repeated using the nearest neighbor nonfeed tree of the same species as the center point. Tissues from feed and nonfeed trees were collected to investigate possible differences in chemical makeup. Tissue samples from feed trees were collected where fresh bark removal indicated the roosting animal had foraged. Samples from nearest neighbor nonfeed trees were taken from branches at the same height and with a diameter similar to those from corresponding feed trees. Bark samples were frozen and analyzed for dietary components. Results from those analyses reasonably approximated values reported for gambel oak (Smith 1957, Kufeld et al. 1981, Welch 1989). Location, slope, aspect, snow depth, and climatic conditions were recorded at each feed tree site. High and low temperature readings were taken daily at an elevation of 1597 m, as well as from the Spanish Fork climatological station.

Laboratory and Statistical Methods

Tissues from feed and nonfeed trees were analyzed for protein and phosphorus using the auto analyzer semiautomated method #12 for feeds (Horwitz 1980). Calcium, magnesium, potassium, and sodium content were determined by the atomic absorption method #2 for plants (Horwitz 1980). Sulphur content was determined by a wet-ash process using nitric and perchloric acid. Crude fiber was determined by the acid detergent fiber and lignin #21 method (Horwitz 1980). An evaluation of crude fat was made using the direct method (Horwitz 1980) on a Lab Con soxlet extractor. A limited number of tissue samples were analyzed on a Hewlett Packard model 5995 gas chromatograph/mass spectrometer (GCMS) for fatty acids and terpenes. Tannin content was measured by the radial diffusion method (Hagerman 1987) with quebracho tannin being the standard, and by astringency (Gambliel et al. 1985). Soluble carbohydrates were determined according to daSilveira (1978). Urine samples of captive porcupines on a strict diet of gambel oak were analyzed for calcium and phosphorus content when laboratory results indicated the Ca/P ratio in the tissue of food materials was greater than expected. Eight oak tissue samples were chosen at random and retested for calcium and phosphorus content according to Horwitz (1980) on a Beckman DU-30 spectrophotometer.

Differences between oak, white fir, and Douglas fir feed and nonfeed trees were statistically analyzed to help discern foraging patterns used by instrumented porcupines. Chemical and ecological factors were evaluated for between-species differences using two-sample *t* tests, and for within-species differences with paired *t* tests (Minitab 1982). Statistical results are reported at the $p < .05$ and $p < .1$ levels. Chi-square analysis was used to determine if utilization of feed tree species by porcupines differed from the expected. Discriminant analysis using backward elimination and forward selection (SAS 1985) was used to determine chemical and ecological factors that best discriminate between tree species, and between feed and nonfeed trees of the same species.

TABLE 1. Mean values for factors tested for possible effects on porcupine herbivory.

	Oak (1)		White fir (2)		Douglas fir (3)	
	Nonfeed tree **n = 46	Feed tree n = 46	Nonfeed tree n = 3	Feed tree n = 3	Nonfeed tree n = 7	Feed tree n = 7
Distance from conifer (m)	—	207	—	0	—	0
Distance to feed tree, same sp. (m)	—	358^{2}	—	543^{1}	—	377
Wind speed (mph)	—	5.5^{3}	—	3.7	—	9.7^{1}
Slope (%)	—	33.5^{3}	—	36.5	—	42.4^{1}
Elevation (m)	—	1779^{2}	—	$1937^{1,3}$	—	1680^{2}
Dbh (cm)	*13.2	$16.5^{2,3}$	*25.4	40.4^{1}	33.3	34.5^{1}
Crude fiber (%)	43.3	44.2^{3}	43.6	48.0^{3}	42.4	$40.1^{1,2}$
Protein (%)	4.9	$5.0^{2,3}$	4.0	4.2^{1}	4.0	3.9^{1}
Phosphorus (%)	0.038	0.039	0.087	0.064	0.038	0.042
Ether extract fractions (%)	9.0	$9.1^{2,3}$	15.7	$12.7^{1,3}$	16.5	$18.9^{1,2}$
Water	41.0	$39.6^{2,3}$	46.1	49.7^{1}	53.4	50.7^{1}
Potassium (%)	0.39	0.39^{3}	0.36	0.31	0.16	0.19^{1}
Calcium (%)	2.7	2.7^{3}	2.8	2.7	1.7	1.7^{1}
Magnesium (%)	0.137	$0.142^{2,3}$	0.083	$0.092^{1,3}$	0.068	$0.065^{1,2}$
Sodium (ppm)	51.1	54.0	53.7	60.0	71.6	58.0
Sulfur (%)	0.20	0.19	0.70	0.48	0.14	0.35
pH	4.7	4.7^{3}	4.7	4.7^{3}	4.3	$4.4^{1,2}$
Tannins (radius in cm)	30.5	$29.6^{2,3}$	17.5	$17.9^{1,3}$	26.2	$25.0^{2,3}$
***Astringency (mg/g fw)	85.8	83.0	*48.7	66.3	104.3	95.8
Sodium salts (%)	2.9	3.0	3.0	3.3	2.9	3.4
Soluble carbohydrates (%)	16.02	16.20	—	—	17.33	16.58
FA (GCMS count units)	827,905	399,239	—	2,609,969	—	1,259,531

Superscript values indicate differences between species at the $p < .1$ level or less. 1 = oak, 2 = white fir, 3 = Douglas fir.

*Values different between feed and nonfeed trees of the same species at or below $p < .1$.

** Multiple locations in the same tree responsible for different n values used in calculations of chemistry and climatic data. Climatic data n values are the same as reported in Table 3.

*** Not comparable across species boundaries.

n values for factors below dashed line not as reported for rest of column. Not statistically comparable due to smaller sample size.

RESULTS

Oak and white fir feed trees were larger than nonfeed trees of the same species ($p < .05$, Table 1). Herbivory by porcupines in deciduous species occurred in the canopies of large trees or in shrubs where branch diameters were relatively small. In coniferous species herbivory was also concentrated in the canopy rather than on the tree bole. Only two instances of chipping bark off the bole to expose the inner bark were noted in our study, both on deciduous tree species. There were no trends correlating calendar date or temperature to selection of feed tree species. Douglas fir feed trees contained greater amounts of crude protein than Douglas fir nonfeed trees ($p < .05$). Crude protein content of both conifer species was less than that of oak trees (Douglas fir $p < .05$, white fir $p < .1$). Total tannins (as measured by radial diffusion) were higher in oak than in conifers (Douglas fir $p < .1$, white fir $p < .05$). Astringency (protein binding capacity) was not comparable among species but was greater for white fir feed trees than nonfeed trees ($p < .1$). Ether extract fractions were lower in oak than in conifers ($p < .05$) and lower in white fir than Douglas fir ($p < .1$).

Tissue from Douglas fir contained less crude fiber than tissue from oak and white fir ($p < .05$), and Douglas fir feed trees contained still less than nonfeed trees ($p < .1$). Water content was lower in oak tissue than in conifer tissue ($p < .05$). Oak contained higher levels of potassium and calcium than Douglas fir ($p < .05$). White fir was also higher than Douglas fir in calcium ($p < .05$). Magnesium levels for oak were greater than for either conifer species ($p < .05$). White fir and oak tissue had higher pH values than tissues from Douglas fir ($p < .05$). Oak feed trees were higher in sodium salts than Douglas fir feed trees ($p < .1$). Calcium-phosphorus ratios for feed trees were higher in oak than in Douglas fir ($p < .05$). The calcium-phosphorus ratio for oak is well above acceptable limits for mineral absorption by mammals

(Underwood 1966). High calcium-phosphorus ratios have also been reported by Masslich (1985) for aspen (*Populus tremuloides*) tissue utilized by beaver. After an independent test of feed tree tissue confirmed the high ratio, we tested the mineral content of feces and urine from captive porcupines on an oak diet. Calcium-phosphorus ratios from fecal material were 10:1, while ratios from urine were approximately 221:1.

Tissue samples from feed trees were analyzed by GCMS primarily as a check on ether extract fractions. The small sample size did not permit statistical analysis, but trends showing lower fatty acid content in oak than in conifers concurred with our observation of lower ether extract fractions in oak. The amount of fatty acids was lower in oak than in either conifer species.

Discriminant analysis correctly classified feed trees as either conifer or oak 100% of the time (Table 2). Six factors were important contributors to the model. Conifer feed trees had higher amounts of phosphorus and a greater ether extract fraction than oak feed trees. Alternatively, oak feed trees were higher in protein, calcium, tannins, and magnesium. Although tannins entered into the model, they were not a significant contributor. These differences between oak and conifer feed trees generally are in agreement with differences in Table 1. The classification of oak feed and nonfeed trees was less successful (71%, Table 2). Oak feed trees were significantly higher in sodium and fiber than nonfeed trees, while nonfeed trees were higher in water content.

Porcupines used gambel oak as a food source more often than it occurred in the study site (p values listed in Table 3). Six of 15 animals were found roosting and feeding exclusively in oak, while 9 roosted and fed in conifer species at least once. Snow depths and temperatures were analyzed for the winter period before the main snowmelt (judged to be 18 March). Average snow depths at porcupine location sites for that time period were 0.60 m. Maximum snow depth was 1.20 m (median 0.65 m). Mean minimum temperature for the night previous to locating study animals was −10°C; the extreme low was −27°C. Mean temperature for the night previous to locating animals in rock or snow caves was −12°C. There was no statistical difference between the minimum nightly temperature previous to locating porcupines in station trees compared to locating porcupines in rock or snow dens.

There were approximately 7.0 porcupines/km^2 in the study area. Radio-collared animals were far ranging and did not utilize a single den or station tree as a base from which to launch foraging expeditions. Rather, they roosted and fed in a single tree for one to several days and then moved to another roost and feeding tree. Death loss due to predation and other causes left only 3 of 5 male and 6 of 10 female porcupines instrumented with radio transmitting devices for the entire winter. This sample size made statistical analysis of home ranges unreliable. Several animals spent the winter in relatively small areas, but most had relatively large, overlapping home ranges. Male home range extremes were 6.8 and 47.5 ha. Extremes for females were 9.2 and 61.8 ha. One female's home range overlapped those of three males and at least four other females. Movements of up to 400–500 m between relocations of some of the larger, mature animals were not uncommon. Some juvenile animals had reduced home ranges and movements, which generally agrees with observations by Roze (1989). Mean distance from oak feed trees to a potential conifer feed tree was significantly less ($p < .05$) than the distance of an average move by a porcupine from an oak feed tree to any other feed tree (Table 1).

Three of 15 porcupines (20%) were eaten by predators in a 4-mo period. Tracks in the snow indicated that one porcupine was pursued, worried, and killed by two coyotes. The other two porcupines eaten by predators died late in the season on south-facing slopes bare of snow; neither the cause of death nor carnivore species could be positively determined. Carcasses of two other porcupines that died presumably of starvation and/or exposure during the course of the study were not scavenged by coyotes.

DISCUSSION

Chemical Factors

Dietary alternatives in the form of different feed tree species, with significantly different chemical makeup, were available to the study population. In winter, vegetative oils have the potential to be the most important source of energy for porcupines. Data from ether extract fractions derived from feed tree tissues indicate

TABLE 2. Standardized canonical discriminant function coefficients for factors that discriminated between oak and conifer feed trees (100% correct classification), and between oak feed trees and oak nonfeed trees (71% correct classification).

Oak (+) vs. conifer (–) feed trees n = 56			Oak feed (+) vs. nonfeed (–) trees n = 46		
	Coefficient	Prob > b		Coefficient	Prob > b
Phosphorous	–1.24	.00001	Water content	–0.62	.006
Ether extract fractions	–0.60	.0001	Sodium	+0.61	.02
Protein	+1.18	.0005	Fiber	+0.59	.001
Calcium	+0.39	.019			
Tannins	+0.29	.175			
Magnesium	+0.24	.006			

that gambel oak, the major food source of our animals, had lower values of ether extract fractions than tissues from conifers. Evaluation of fatty acids by GCMS confirmed that fatty acid content was higher in conifer tissue. Additional research on known digestible fractions is needed, but until data indicating otherwise are presented, we will operate under the premise that for porcupines conifers provide a greater source of useable fats than do oaks. Discriminant analysis was used to determine if, when all variables were taken together, there would be general support from this analysis with the *t* test. Significant differences found by these analyses comparing oak and conifer feed trees were in agreement (Tables 1, 2). Phosphorus and the ether extract fraction were higher in conifer feed trees compared to oak feed trees, and protein, calcium, tannins, and magnesium were higher in oak feed trees. Discriminant analysis was less successful in classifying feed and nonfeed trees within oak (Table 2). An important reason for this less successful classification was that the cloning nature of oak was emphasized by the point-quarter method. This method may have resulted in selecting nonfeed trees from the same clone as the feed tree. Future research should involve delineating the boundary of the clone and selecting a nonfeed tree from a clone different from the feed-tree clone.

Conifer roost sites also offer greater thermal advantages than deciduous roost sites (Clarke and Brander 1973, Roze 1989). Despite multiple options, porcupines depended heavily on an oak diet low in fats and associated thermal advantages but higher in tannins. The advantage of the oak diet may well be that it is higher in protein. High levels of crude fiber (e.g., cellulose) reduce the digestibility of crude protein in monogastrics (Glover and Duthie 1958a, 1958b). Therefore, herbivores on a high-fiber diet would be expected to maximize the intake of crude protein to compensate for a low digestibility rate. Implications of a diet high in calcium and tannins are less clear, but it is possible that porcupines may deal with high levels of calcium in their food material by concentrating calcium in the urine. Tannins function as protein binding agents (Rhoades and Cates 1976). It is now evident that some insects can circumvent tannins through a higher gut pH and the presence of surfactants (Bernays 1981, Martin and Martin 1984, Martin et al. 1985). However, pH values for the mid-caecum (6.6), and the pyloric (1.8) and esophageal (3.2) regions of the stomach of a laboratory porcupine on a diet of oak were consistent with gut pH for monogastrics of comparable size (Hume 1982).

Oveson (1983) measured subcutaneous adipose concentrations on the rump of porcupines and reported a thickness of 15.1 mm (± 2.6 mm) in early winter. By late February and early March fat reserves were virtually nonexistent. A similar phenomenon was observed by Sweitzer and Berger (1993) in Nevada, where porcupine body condition decreased significantly throughout the winter season. Those authors suggested the change in body mass was an indication that porcupines depleted energy reserves early in the winter and were stressed nutritionally during late winter. The heavy accumulation of fat serves as an energy reserve for porcupines to draw upon throughout the winter, allowing them to concentrate on a food source relatively high in crude protein. The reduced capabilities of protein digestibility associated with a high-fiber diet may have encouraged our study animals to maximize dietary protein by selecting oak.

Porcupine herbivory was generally noted on small branches. In large trees porcupines fed high in the canopy where limbs are smaller.

Table 3. Chi-square analysis of percent occurrence and utilization of trees by porcupines.*

	% occurrence	% used	Chi-square value	p value
Oak	43.5	82.1	3.23	0.10
Conifer	2.7	16.4		
Maple	52.1	1.5	52.41	0.01
Conifer	2.7	16.4		
Oak	43.5	82.1	59.14	0.01
Maple	52.1	1.5		

*n values differ from those reported in Table 1 due to the extended use of some feed trees by porcupines. Occupancy of the same feed tree during more than one sampling event counted as multiple utilization of oak but not double sampled for chemistry data. Df = 1.

We observed only two instances in which porcupines chipped bark of large tree boles and fed on tissue from large dbh limbs or trunks. Selection of larger feed trees by porcupines may be related to the texture of bark and ease of climbing (Roze 1989) rather than chemistry.

Deciduous Food and Roosting Resource

Roze (1989) discussed the thermal advantages of dens and/or conifer roost trees in relation to maintenance of a core body temperature. Citing Irving et al. (1955) and Clarke (1969), he indicated that the critical external temperature below which porcupines must increase their metabolic rates to maintain a core body temperature is a range between –12 and –4°C. He suggested dens are temperature-averaging devices that protect porcupines against convectional and radiational heat loss. Station trees provide thermal advantages to porcupines (Clarke and Brander 1973) and may serve as a substitute for rock caves and snow dens. However, none of these are requisite to porcupine survival. Roze (1989) noted that porcupines may spend winters in trees away from dens and that in every report the tree species have been evergreens.

Our data conflict with this observation. Porcupines throughout western North America are able to survive using a variety of deciduous species as food and roost tree resources. Despite the prominence of literature concerning dens and conifer station trees, use of a deciduous food and roosting resource without dependence on caves or snow dens is not an anomaly for porcupines. Craig and Keller's (1986) study site in southern Idaho was at an elevation of 1525–2089 m in desert shrub habitat. Animals in this study were not observed using dens during the winter or following runways in feeding areas. They remained in the tops of hawthorne (*Crataegus douglasii*) thickets or utilized other deciduous food sources throughout the winter. Sweitzer and Berger (1993) identified buffalo-berry (*Shepherdia argentea*), willow (*Salix spp.*), bitterbrush (*Purshia tridentata*), and juniper (*Juniperus osteosperma*) as primary winter food sources of porcupines in Nevada. We have also observed the extensive use of hackberry (*Celtis occidentalis*) and green ash (*Fraxinus pennsylvanica*) by porcupines as a food and roosting resource in the Sand Hills of Nebraska and the Missouri River Breaks of South Dakota. Caves and conifers (except plantation forests and eastern red cedar [*Juniperus virginiana*]) are not available in the Sand Hills (Swinehart 1989). Oveson (1983) reported that a porcupine remained virtually motionless while perched in a gambel oak tree for a 24-h period when the ambient temperature was as low as –37°C. During a 13-d period from 30 January through 11 February, when the mean low temperature was –17°C, 3 of 25 (12%) locations of our study animals were in conifers, 4 (16%) were in rock or snow caves, and 18 (72%) were in oak. Although porcupines did select trees with a larger dbh as roosting/feeding sites, they were also often found in smallish shrubs even though large trees were readily available. It is therefore difficult to link possible benefits presumed to be available to porcupines that roost in larger trees, such as protection from the elements or from predators, to the selection shown by animals in this study.

Despite the availability of snow caves, dens, and conifer species that could provide thermal advantages, the study population was heavily dependent on gambel oak for a roosting and feeding resource. Considering that this reliance was during a season of energetic stress, it is likely that remaining motionless in the canopy of oak trees to conserve energy while exploiting a high-protein food source is an adaptive strategy.

Movements and Predation

The availability of conifer feed trees was not limiting since the average distance between locations of study animals was significantly greater than the mean distance of a move from any roost tree to a conifer roost tree (Table 1). It does not appear that spatial relationships of the various feed tree species played a role in feed tree selection by our study population. The relatively large overlapping winter home ranges of animals in this study differ from reports of other researchers. Home ranges for porcupines in northwestern Minnesota were small enough to be reported in square meters (Tenneson and Oring 1985). Curtis (1941), Dodge (1967), Brander (1973), Roze (1987, 1989), and others have documented that porcupines move short distances from dens to feed trees, sometimes along permanent trails in the snow. Craig and Keller (1986) and Smith (1979) also reported reduced ranges in the winter. However, Dodge and Barnes (1975) did not indicate a similar restriction in winter movements. Roze (1987) suggested the reason may be crusted snows that bear the weight of the animals. Porcupines in our study did adeptly toboggan on crusted snows down extreme slopes in an attempt to avoid capture. However, one female moved over 450 m in fresh snow. Trails in powdery snow were often direct and suggested that a destination may have been predetermined.

Common use of oak and conifer feed trees by different porcupines occurred several times during the study, sometimes concurrently. Hedging in the canopies of gambel oak trees indicated that some trees were used consistently over time by porcupines while others were not. Consistent foraging in common trees over time may indicate a learned behavior such as that described by Glander (1981) for howler monkeys, but we hesitate to attribute it to such because porcupine young-of-the-year were usually separated from their mothers during the winter. It is possible that some young accompanied their mothers for limited periods in the winter or that more subtle cues were used to transfer the information.

Long movements between feed trees in dense oak cover by some study animals suggest that predator-prey relationships may have influenced movements. Sweitzer and Berger (1992) found that habitat use was related to the age or size class of porcupines, presumably in response to increased risk of predation to smaller porcupines. Our observations generally agree with their findings. Mountain lion and coyote tracks were seen regularly in the study area. Both species are known to prey on porcupines (Keller 1935, Robinette et al. 1959, Toweill and Meslow 1977, Maser and Rohweder 1983). The strong urine scent at station trees or dens makes porcupines readily detectable. Mountain lions are capable of knocking porcupines from the canopies of trees (Taylor 1935). If long moves decreased the predictability of mountain lions locating porcupines in station trees, it would be an adaptive strategy. However, long moves expose porcupines to terrestrial predation by mountain lions, coyotes, and wolves (*Canis lupis*, which are now extirpated from the study area) and would presumably be nonadaptive. Since ample forage exists throughout the study site and long moves to locate food resources do not appear to be a dietary necessity, long movements may be an adaptive strategy to avoid arboreal predation by mountain lions. This hypothesis deserves further examination.

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HISTORIC EXPANSION OF *JUNIPERUS OCCIDENTALIS* (WESTERN JUNIPER) IN SOUTHEASTERN OREGON

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ABSTRACT.—The chronology of *Juniperus occidentalis* (western juniper) expansion in eastern Oregon, the effect of plant canopy and interspace on *J. occidentalis* seedling establishment and growth rates, and the age of *J. occidentalis* maximum reproductive potential were determined. Measurements were recorded in twenty-two 0.4-ha plots established in sagebrush-grassland communities and six 0.1-ha plots in *Populus tremuloides* (quaking aspen) communities. *J. occidentalis* began increasing during the 1880s in stands containing trees >130 yr old. Relatively steady establishment ensued into the 1950s and then began to progress at a geometric rate in the 1960s. *J. occidentalis* encroachment into aspen stands began between 1910 and 1920. The largest proportion of juvenile trees established beneath *Artemisia* species in sagebrush-grassland communities. *J. occidentalis* trees appeared to reach full reproductive potential at >50 yr of age. The ratio of male:female trees increased from 1.7 in scattered *J. occidentalis* stands to 3.8 in closed stands. The initiation of *J. occidentalis* encroachment during the late 1800s coincides with optimal climatic conditions for *Juniperus* berry production and establishment, reduced fire-return intervals, and heavy livestock grazing. The accelerated increase in *J. occidentalis* expansion since 1960 may be due to the continued absence of fire, abundant woody plant cover, and the large increase in *J. occidentalis* seed production.

Key words: western juniper, Juniperus occidentalis, *expansion, Great Basin, intermountain shrub steppe, aspen,* Populus tremuloides, *succession.*

One of the most pronounced plant community changes in the 20th century has occurred in the juniper and pinyon-juniper woodlands, a major vegetation type characterizing the Intermountain Region. These woodlands, sometimes described as pygmy forests, currently occupy 17 million ha throughout this region (West 1988). *Juniperus occidentalis* ssp. *occidentalis* Hook. (western juniper) is considered the Northwest representative of the pinyon-juniper zone in the Intermountain Region (Franklin and Dyrness 1973) and occupies over 1 million ha (Dealy et al. 1978) in eastern Oregon, southwestern Idaho, and northeastern California (Cronquist et al. 1972). This subspecies of *J. occidentalis* is found primarily north of the polar front gradient (Neilson 1987; parallel to the Oregon and Nevada border, latitude 42°) where temperatures are cooler, summer precipitation decreases, and winter precipitation increases (Mitchell 1976).

Relict juniper woodlands, tree-age class distribution, fire scars, and historical documents indicate presettlement pinyon-juniper and juniper woodlands were usually open, savannah-like (Nichol 1937, West 1988), or confined to rocky surfaces or ridges (Cottam and Stewart 1940, Barney and Frishknecht 1974, Hopkins 1979, Johnson and Simon 1987). *J. occidentalis* began increasing in both density and distribution in the late 1800s (Burkhardt and Tisdale 1976, Young and Evans 1981, Eddleman 1987), invading *Artemisia tridentata* subsp. *vaseyana* (mountain big sagebrush), *Artemisia arbuscula* (low sagebrush), *Populus tremuloides* (quaking aspen), and riparian communities. Although *J. occidentalis* is long lived (Vasek 1966, Lanner 1984), less than 3% of the woodlands in Oregon are characterized by trees >100 years old (USDI-BLM 1990). In 1825, Ogden observed only occasional *J. occidentalis* (reported as cedars) growing on hillsides while traveling through the Crooked River drainage in central Oregon (Rich et al. 1950). Today, these hillsides are covered by dense *J. occidentalis* woodlands. In a nearby area J. W. Meldrum's 1870 survey notes describe a gently rolling landscape covered with an abundance of perennial bunchgrasses and a wide scattering of *J. occidentalis* trees (Caraher 1977). Today, *J.*

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occidentalis densities on this site range between 125 and 250 ha^{-1}. In Silver Lake, Oregon, *J. occidentalis* density increased from 62 ha^{-1} in 1890 to over 400 ha^{-1} by 1970 (Adams 1975). On another site in central Oregon where trees were absent prior to 1880, *J. occidentalis* increased to 1018 ha^{-1} by 1980 (Eddleman 1987). Recent expansion is similar to increases in other *Juniperus* species throughout western United States (Ellis and Schuster 1968, Tausch et al. 1981, West 1984, Tausch and West 1988).

The objectives of our study were to (1) describe the chronology of *J. occidentalis* expansion during the past several centuries in southeastern Oregon, (2) determine the effect of plant canopy and interspace on *J. occidentalis* seedling establishment and growth rates, and (3) determine the age when *J. occidentalis* reaches maximum reproductive potential.

METHODS

Study Area

The study area is located on Steens Mountain in southeastern Oregon, approximately 80 km south of Burns. This isolated volcanic fault-block, which lies in the extreme northwest Basin and Range Province (Fenneman 1931), is about 80 km long and oriented in a northeast direction (Baldwin 1981). The elevation of Steens Mountain ranges from 1268 to 2949 m, with a steep east-facing escarpment and a gentle west-facing slope. Climate is cool and semiarid, characteristic of the northern Great Basin. Annual precipitation at the lower elevations averages 220–280 mm, increasing to ≥ 700 mm at higher elevations (NOAA 1993). Most moisture is received as snow in November, December, and January and as rain in March through June.

J. occidentalis woodlands on Steens Mountain form a discontinuous belt between 1450 and 2100 m in elevation. Severe winter conditions probably restrict *J. occidentalis* from expanding into higher elevations (Billings 1954, Mehringer 1987). Limited distribution below 1500 m is possibly due to a combination of late spring frosts (Billings 1954) and limiting moisture. Tree canopy cover varies from open to 30% cover, except on mesic *P. tremuloides* sites where *J. occidentalis* cover approaches 100%. However, based on age structure and canopy leader growth, tree canopies are still actively expanding on the majority of sites measured. Early observations on Steens Mountain indicate the landscape contained only scattered stands of *J. occidentalis* (Griffiths 1902). Since 1900 the abundance of *J. occidentalis* pollen in the Steens Mountain area has increased fivefold (Mehringer and Wigand 1990).

Plant communities characteristic of *J. occidentalis* woodlands are *Artemisia tridentata* ssp. *vaseyana/Festuca idahoensis* (Idaho fescue), *Artemisia arbuscula/F. idahoensis*, and *P. tremuloides*. *P. tremuloides* communities on Steens Mountain range in elevation from 1760 to 2400 m. At lower elevations, in the *J. occidentalis* woodland belt, *P. tremuloides* stands form long, narrow communities along north aspects, which capture windblown snow and runoff.

Plot Layout

Plot locations were selected in an attempt to reflect sagebrush-grassland communities in different stages of *J. occidentalis* invasion on the west slope of Steens Mountain. Old stands on the rocky outcrops, which make up only a small percentage of present-day woodlands, were not measured. Sites selected support, or have the potential to support, sagebrush-grassland communities. Currently these sites are occupied by varying numbers and sizes of *J. occidentalis* dominance, creating a woodland structure of dispersed, intermediate, and closed tree stands (Table 1). Twenty-two 0.4-ha plots were located within the *J. occidentalis* belt of Steens Mountain; they ranged from 1500 to 2000 m in elevation and were distributed 32 km along the mountain range. Plots were situated along an elevation gradient representing communities from the lower- to upper-elevation *J. occidentalis* woodland belt. Dominant understory vegetation in the dispersed and intermediate plots was *A. tridentata* spp. *vaseyana* and *Festuca idahoensis* (13 stands), *A. arbuscula* and *F. idahoensis* (4 stands), and a mosaic of *A. arbuscula* and *A. tridentata* ssp. *vaseyana* (2 stands). Understory vegetation in the closed stands (n = 3) comprised a few remnant deep-rooted perennial grasses, skeletons of dead *A. tridentata* ssp. *vaseyana*, and 70% bare ground (EOARC data file).

An additional six 0.1-ha plots were established in six separate *P. tremuloides* stands. Three stands were in advanced stages of *J. occidentalis* invasion with few to no adult *P.*

TABLE 1. *Juniperus occidentalis* stand maturity classes in *Artemisia* communities (modified from Blackburn and Tueller 1970).

Closed	Abundant adult trees generally >5 m tall and usually several trees >130 yr of age, with little understory, particularly on south slopes.
Intermediate	Abundant *J. occidentalis* of all age classes, with a more open tree canopy and an understory beginning to decline; trees >130 yr of age are rare.
Dispersed	Abundant young trees <2 m tall, a few adult trees but old trees absent, and a well-developed understory.

tremuloides trees and dead *P. tremuloides* trunks on the ground. The remaining three stands were characterized by a dominant *P. tremuloides* overstory and an understory of young *J. occidentalis*. Elevation for the *J. occidentalis–P. tremuloides* plots ranged from 1930 to 2000 m, all with a similar northeast aspect.

Measurements

Prior to sampling, string was stretched along the contour of each 0.4-ha plot at 1-m intervals to keep track of measured trees. *J. occidentalis* density (trees ha^{-1}) was recorded for trees <0.5 m tall, defined as adult, across the entire plot. Tree height, minimal and maximal crown diameters, and basal area just above the trunk swell at the stem base near the litter layer were recorded. Tree height was measured with a tape for trees ≤ 2 m and a clinometer for trees >2 m tall. Tree canopy cover was estimated by adding crown area measurements of all trees for each plot. Similar measurements were recorded on juvenile trees (defined as trees ≤ 0.5 m tall), but only those on the lower left quarter (0.1 ha) of each 0.4-ha plot. Current-year *J. occidentalis* seedlings (any plant with cotyledons still attached) were not recorded. Establishment location of each juvenile tree was recorded: beneath the canopy of *J. occidentalis*, *Artemisia*, other shrubs, tussock grass, or in the interspace. Less than 1% of juveniles were located beneath other shrubs or grasses; therefore, only *J. occidentalis*, *Artemisia*, and interspace are reported.

J. occidentalis is considered submonoecious (Vasek 1966). Male and female reproductive status was determined by estimating abundance of cones and berries for each tree. Abundance was ranked in four classes: (0) absent, (1) scarce, (2) obvious but not abundant, and (3) abundant.

In each plot a 10-tree subsample was randomly selected for aging in each of four height classes: (1) <0.5 m, (2) 0.5–1.8 m, (3) 1.8–3 m, and (4) >3 m. In several of the dispersed plots, sample size for trees >3 m was smaller than 10, due to a lack of trees. We also sampled all old trees on plots when they occurred (n = 0–5 ha^{-1}). Old trees were easily identified by their growth form, containing rounded tops and heavy limbs, and lacking strong terminal leader growth (Burkhardt and Tisdale 1969). A cross section was removed approximately 30 cm above ground level from each tree >0.5 m tall and at ground level for trees ≤ 0.5 m, and then brought back to the lab for aging. Two radii from each cross section were polished, stained, and counted. Age was estimated by averaging both radii and adding 10 yr to correct for the 30-cm base. Mean differences between radii were 4% for trees >50 yr and 1% for trees ≤ 50 yr of age. Adams (1975) reported that growth-ring characteristics of *J. occidentalis* are useful in dendrochronological studies. The presence of false and missing rings was similar to that for *Pinus ponderosa*. Over 1200 trees were aged and approximately 14,000 counted and measured. In the six *P. tremuloides* stands, density of both *J. occidentalis* and *P. tremuloides* and age and height for *J. occidentalis* were measured across the entire 0.1-ha plot.

Evidence indicated minimal *J. occidentalis* mortality has occurred on Steens Mountain during the past 120 years. We observed very few dead or dying trees for all age classes (excluding seedlings), except where individual *J. occidentalis* trees had been cut or burned. Mortality of *Juniperus* species rapidly declines following the seedling stage (Van Pelt et al. 1990). *Juniperus* has few pests that prove fatal to the tree (Lanner 1984). We avoided recently cut or burned stands, which constituted a small percentage of *J. occidentalis*–occupied stands. Where remains of dead trees were observed, we noted they persisted for a long period of time. By recutting several stumps adjacent to one of our plots and aging and matching ring widths with adjacent live trees, we determined these trees were harvested around 1920. Others have also observed the persistence of *Juniperus* stumps (Young and Budy 1979).

Statistical Analysis

Height growth data for adult trees were analyzed using a randomized complete block design in PROC GLM of SAS (SAS 1986). Means were separated using Duncan's Multiple Range Test at $p \leq .05$ level. A split-plot design was used in the analysis of juvenile height growth. Main plots were sites and subplots were location of establishment (interspace, *Artemisia*, *J. occidentalis*). A Duncan's Multiple Range Test was used to separate the means.

RESULTS

Little change in *J. occidentalis* density appeared to occur between the early 1700s and the 1880s (Fig. 1). We encountered old trees (standing trees >130 years old, large stumps, and burned-out trunks) on several *A. arbuscula* flats and *A. tridentata* ssp. *vaseyana* communities. However, data indicated presettlement tree densities in these *Artemisia* communities were ≤ 5 trees ha^{-1}, suggesting very open *J. occidentalis* stands. The first evidence of an increase in tree densities occurred in the 1880s, with relatively steady establishment ensuing into the 1950s, similar to that observed by Tausch and West (1988). In the 1960s *J. occidentalis* establishment began occurring at a geometric rate.

Closed *J. occidentalis* stands, which once supported *A. tridentata* ssp. *vaseyana*, were characterized by an abundance of adult trees (≥ 3 m tall), a tree canopy cover of 18–28% (Table 2), and the presence of a few old trees (130+ yr; 2 to 5 ha^{-1}). *J. occidentalis* densities began increasing in these stands between 1878 and 1890. In the intermediate *J. occidentalis* stands, trees >130 yr were rare. Tree canopy cover ranged from about 8 to 16%, and densities of adult trees varied from 35 to 100 ha^{-1}. Trees <3 m in height, particularly juveniles, were abundant. *J. occidentalis* expansion in these sagebrush-grassland communities began between 1890 and 1910. In the dispersed stands few trees were >60 yrs old, and we aged no trees >100 yr. Tree canopy cover was usually <5% in the dispersed stands and densities of large adult trees <35 ha^{-1}. Invasion of *J. occidentalis* into these sagebrush-grassland communities began after 1930.

Greatest densities of *J. occidentalis* trees measured on Steens Mountain occurred in *P. tremuloides* sites (Table 3). In the late stages of *J. occidentalis* succession on these sites, tree canopy cover approached 100%. Live *P. tremuloides* occurred only on one of the three sites, and almost all trees were <0.5 m tall. In the remaining two stands only the remnants of large *P. tremuloides* trunks decaying in the understory were present. *J. occidentalis* invasion in these *P. tremuloides* sites began between 1910 and 1920. No *J. occidentalis* trees

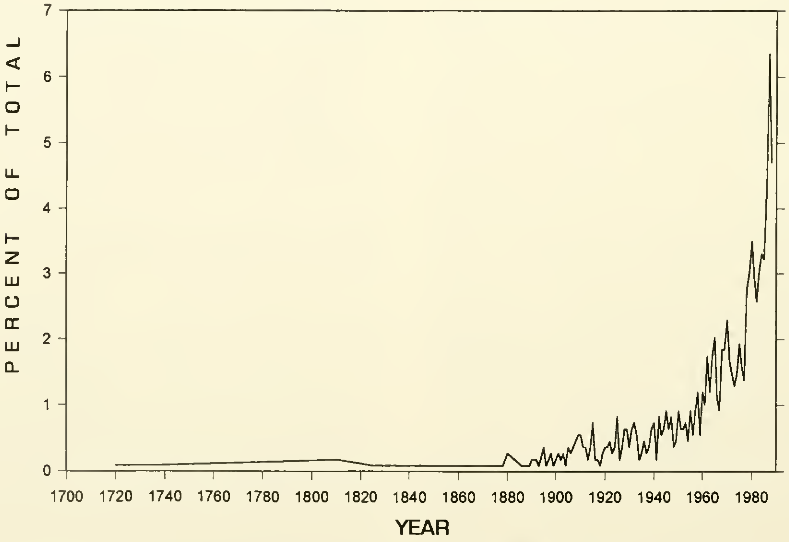

Fig. 1. Years of establishment for *Juniperus occidentalis* trees on Steens Mountain, Oregon (n = 1200).

TABLE 2. General description of closed, intermediate, and dispersed *Juniperus occidentalis* stands on Steens Mountain in *Artemisia tridentata* ssp. *vaseyana* and *A. arbuscula* communities, and the percentage of juveniles located beneath *J. occidentalis*, *Artemisia*, and interspace. Canopy cover, basal area, and density means are followed by range in parentheses ( ).

				Density (#ha^{-1})		Establishment site % (for juveniles)		
	# sites	Canopy cover %	Basal area (m^{2}ha^{-1})	Adults >0.5 m ht	Juveniles <0.5 m ht	*J. occidentalis*	*Artemisia*	Interspace
A. tridentata ssp. *vaseyana*								
closed	6	22 (18–28)	5.2 (3.1–9.8)	296 (217–496)	580 (118–1226)	86^{a1}	9^{b}	5^{b}
intermediate	8	6 (5–10)	1.8 (0.5–4.7)	95 (50–165)	815 (335–1423)	29^{b}	58^{a}	13^{c}
dispersed	2	2 (1–3)	0.4 (0.2–0.6)	52 (31–70)	188 (96–280)	3^{b}	50^{a}	47^{a}
A. arbuscula								
closed	3	15 (12–20)	3.5 (1.8–5.4)	158 (74–247)	99 (20–198)	27^{b}	67^{a}	6^{c}
intermediate	3	6 (4.5–6.7)	1.8 (0.9–3.2)	104 (77–153)	375 (167–790)	11^{b}	61^{a}	28^{b}

[1] Sites of establishment means (%) followed by similar lowercase letters are not significantly different between establishment sites within *J. occidentalis* stand maturity classes ($p \leq .05$).

>80 yr were encountered. In stands with a *P. tremuloides* overstory, *P. tremuloides* density of small shoots was greater than that of *J. occidentalis*. However, *P. tremuloides* size classes between 0.5 m and large adults were absent, indicating a lack of *P. tremuloides* stand rejuvenation. On these sites *J. occidentalis* invasion began between 1930 and 1940.

Height growth for young *J. occidentalis* trees (<20 yr) across all sites averaged 2.9 cm yr^{-1}. Based on growth rates and height of trees between 10 and 20 yr of age ($n = 200$) across all *Artemisia* sites, 90% of trees 15 yr old were <1 m tall (64% were <0.5 m tall). Surprisingly, height growth rates of juvenile trees did not significantly differ between *A. arbuscula* and *A. tridentata* ssp. *vaseyana* communities. However, location of establishment within communities significantly influenced growth rates of young *J. occidentalis* trees (Table 4). Trees establishing beneath an *Artemisia* canopy grew faster than young trees growing in the interspace.

Shrub and tree canopies also significantly influenced location of *J. occidentalis* seedling establishment in *Artemisia* communities. The largest proportion of juvenile trees was usually located beneath canopies of *A. tridentata* ssp. *vaseyana* or *A. arbuscula* and *J. occidentalis* (Table 2). Less than 20% of juveniles across all 22 *Artemisia* sites established in the interspace.

On Steens Mountain, for trees >0.5 m tall, 32% expressed predominantly only male or only female characteristics, 38% both male and female, and 30% contained neither fruits nor cones. *J. occidentalis* trees producing abundant crops of cones or berries were either male or female dominant. No trees were measured which contained an abundant crop of both berries and cones. Sixty-five percent of *J. occidentalis* trees with an abundant crop of berries contained no male cones. The remaining 35% contained only a scarce number of cones. The majority of trees producing abundant crops of male cones contained only scarce numbers of berries. Approximately 75% of trees producing heavy crops of berries or cones were >50 yr old. Trees <20 yr old expressing reproductive effort were rare and produced only a few cones or berries. The ratio of trees producing large crops of cones versus berries (cones:berries) increased from 1.7 in the scattered *J. occidentalis* stands to 3.8 in the closed stands.

DISCUSSION

Low densities and limited distribution of *J. occidentalis* trees >130 yr and limited numbers of dead trees or old stumps suggest *J. occidentalis* has greatly expanded on Steens Mountain during the past 100 yr. Distribution of old trees was generally limited to rocky ridges and *A. arbuscula* communities. Old trees were found only occasionally growing in deeper, well-drained soils such as *A. tridentata* ssp. *vaseyana* grassland communities and were absent in *P. tremuloides* communities. In northeastern California, Barbour and Major

TABLE 3. Mean densities (# ha^{-1}) followed by range in ( ) of *Populus tremuloides* and *Juniperus occidentalis* in *P. tremuloides* sites.

Stage of succession	*P. tremuloides*		*J. occidentalis*	
	Adult	Juvenile	Adult	Juvenile
Late (*n* = 3)	17 (0–50)	1316 (0–3952)	1392 (929–2203)	9462 (4327–18,791)
Intermediate (*n* = 3)	1060 (476–1670)	6553 (5266–9480)	1090 (632–1739)	2816 (622–5968)

(1977) found a similar distribution of old and young *J. occidentalis* trees. *A. tridentata* ssp. *vaseyana* and *A. arbuscula* communities, which contained a low density of *J. occidentalis* trees prior to settlement, were the earliest sites to initiate an increase in *J. occidentalis*. Dates of initial establishment of closed and intermediate stands were similar to periods of early stand development reported by Young and Evans (1981) in northeastern California and Eddleman (1987) in central Oregon.

Expansion of *J. occidentalis* coincides with Euro-American settlement in this portion of the Great Basin. Although no direct cause-and-effect relationship can be drawn, we hypothesize that climate, altered fire frequencies, and grazing in the late 1800s were primary factors initiating the recent expansion of *J. occidentalis*. Following the end of the Little Ice Age in the mid 1800s (Bryson 1989), winters became more mild and precipitation increased above the present long-term average in the northern half of the Great Basin between 1850 and 1916 (Antevs 1948, Graumlich 1985). Mild, wet winters and cool, wet springs promote vigorous growth in *J. occidentalis* (Earle and Fritts 1986, Fritts and Xiangdig 1986).

Presettlement fire-return intervals in *A. tridentata* ssp. *vaseyana* communities have been reported to vary from 15 to 25 yr (Houston 1973, Burkhardt and Tisdale 1976, Martin and Johnson 1979). Burkhardt and Tisdale (1976) concluded that fire-frequency intervals of 30–40 yr would be adequate to keep *J. occidentalis* from invading a sagebrush-grassland community. Following settlement, frequency of fire in sagebrush grasslands has greatly declined. The reduction of fine fuels by high densities of domestic livestock greatly reduced the potential for fire in the Intermountian Shrub Region (Burkhardt and Tisdale 1976, West 1988). Griffiths' (1902) observations of the overgrazed landscape on Steens Mountain support this hypothesis. Fires set by Native Americans also declined in the 19th century due to large reductions in their populations caused by European diseases (Thompson 1916, Cressman 1981) and relocation to reservations in the 1870s.

The invasion of conifers into *P. tremuloides* communities is a common occurrence throughout the western U.S. However, conifers reported to typically invade *P. tremuloides* stands are species adapted to more mesic sites such as *Pinus contorta* (lodgepole pine), *P. ponderosa*, *Pseudotsuga menziesii* (Douglas-fir), *Abies concolor* (white fir), *Abies lasiocarpa* (subalpine fir), *Picea engelmannii* (Engelmann spruce), and *Picea pungens* (blue spruce) (Bartos 1973, Mueggler 1985). Invasion of the more drought-tolerant *J. occidentalis* into *P. tremuloides* stands is not well documented.

P. tremuloides is frequently considered a fire-induced species, replaced by less fire tolerant conifers (Baker 1925, Daubenmire 1943, Mueggler 1976). Prior to settlement, lightning and human-set fires probably helped maintain many *P. tremuloides* communities. However, the occurrence of fire in *P. tremuloides* stands in the Rocky Mountains has been greatly reduced since the late 1800s (Jones and DeByle 1985). Mueggler (1985) suggested the combination of fire suppression and heavy grazing in *P. tremuloides* communities may favor the establishment of conifers.

An increase in *Artemisia* cover may also enhance the invasion of *J. occidentalis*. As a sagebrush-grassland community shifts towards a greater dominance of shrubs, the number of safe sites for *J. occidentalis* seedling establishment increases. Others have also reported the majority of *J. occidentalis* seedlings established beneath *Artemisia* canopies (Burkhardt and Tisdale 1976, Eddleman 1987). In west Texas, *J. pinchotii* frequently establishes beneath mesquite plants (McPherson et al. 1988).

TABLE 4. Mean growth rates for juvenile *Juniperus occidentalis* trees (2–30 yr old) in three different establishment sites.

Establishment site	cm yr^{-1}
Artemisia	3.3^{A}
J. occidentalis	2.7^{AB}
Interspace	2.4^{B}

Means followed by similar uppercase letters are not significantly different ($p \leq .05$).

Shading by nurse plants may benefit *J. occidentalis* seedlings (Johnsen 1962) by reducing summer surface temperatures by 45–57% of bare ground surface temperatures (Burkhardt and Tisdale 1976). Enhanced growth rates of young trees growing beneath *A. tridentata* ssp. *vaseyana* suggest microclimates beneath shrub canopies are more beneficial than conditions in the interspace. Burkhardt and Tisdale (1976) reported *J. occidentalis* seedling growth rates were correlated positively with *Artemisia* and correlated negatively with bare ground.

J. occidentalis approached full reproductive potential near 50 yr. As *J. occidentalis* densities increased, the proportion of trees became predominantly male across sites. Highly fecund female trees appeared to be most important in open stands where *J. occidentalis* was actively expanding. In central Oregon, Eddleman (1984) observed that trees in the interior woodlands were strongly dominated by male cone production while trees growing in the open produced more female cones. He also reported trees did not produce significant quantities of fruit until 50–70 yr of age.

Conclusion

Optimal climatic conditions around the turn of the century, reduced fire return intervals, and the indirect effect of livestock through the reduction of fine fuels and an increase in *Artemisia* cover are probably primary factors that have contributed to the rapid expansion of *J. occidentalis* in southeast Oregon during the late 1800s and early 1900s. The accelerated increase in *J. occidentalis* density and invasion during the last 30 years into new communities is probably largely due to the continued absence of fire, abundant woody plant cover, and the large increase in *J. occidentalis* seed rain.

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RANGELAND ALPHA DIVERSITIES: HARVEY VALLEY, LASSEN NATIONAL FOREST, CALIFORNIA[1]

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ABSTRACT.—Monitoring diversity usually begins by estimating alpha diversity of a plant community on a specific site. The objectives of this study were to provide alpha diversity benchmarks and to determine whether rangeland community basal cover characteristics explained variation in diversity estimates. Plant and surface component cover percentages were estimated on 51 plots (representing four vegetation types) on the Lassen National Forest, CA. Each plot was sampled with 30 random, 102 basal point transects. Jackknife procedures were used to compute means and standard errors for Margalef's diversity index (D_m), which stresses species richness, and Simpson's index (D_s), which stresses species dominance. Within vegetation types, D_m and D_s did not rank all plots in the same order. Highest D_m values occurred with the most species. Highest D_s values occurred with comparatively few species but more uniform cover. With either index, average diversity declined from the meadow to grassland to open shrub-grass to timber-bunchgrass types. All possible subset regressions of diversity on the basal cover characteristics were computed. Portions of the variance accounted for by the best models were too low to allow prediction of D_m and D_s. The relation of alpha diversity to rangeland health is discussed.

Key words: ecology, plant communities, Margalef's index, Simpson's index, monitoring, basal cover.

Biological diversity (hereafter called diversity) involves ecological processes, structures, and functions and may occur at any spatial scale (Society of American Foresters 1992). Diversity refers to variety and abundance; it is variety or multiformity—of different forms or kinds (Stein and Urdang 1966). There are alpha, beta, and gamma diversities (Whittaker 1972). Alpha diversity is the variety that occurs within a plant community of a specific site. A site or stand is defined as an individual unit that is homogeneous in vegetation, soil, topography, microclimate, and history (West 1993). Beta diversity is the variety of communities along a gradient (e.g., topography, soil acidity, or moisture regime) or on a given site through time. Gamma or large-scale diversity is the variety of plant communities, or the total number of species present, or both in a specific geographic area (e.g., grazing allotment or watershed).

Diversity has two components, richness and evenness (Ludwig and Reynolds 1988, Magurran 1988). Richness refers to variety (numbers) of species, for example. Evenness refers to equality (abundance or numbers) of species botanical composition, for example.

Diversity may or may not follow traditional concepts of succession and increase from pioneer to climax plant communities or decrease with rangeland deterioration. Over large areas diversity may be higher if communities are at several seral stages than if the entire area is at a single seral stage. Within specific sites physical/chemical factors or intense competition or both may work to reduce diversity (Odum 1959). Absence of an expected species may be due to frequent disturbances, a low immigration potential, an immature soil, or an inhospitable moisture regime (del Moral and Wood 1988).

Nevertheless, because it may change with the kind of management, diversity should be assessed as part of range health evaluations. Diversity indices provide information that may not be immediately apparent from basic measures of the plant community such as cover and composition. High diversity of plant species is important in maintaining processes and flow pathways for energy and nutrients within and among communities. Higher diversity implies a greater number of occupied niches (Whittaker 1972).

Protecting or enhancing diversity, or both, are goals commonly set by policy or law. West

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(1993) gave four reasons for having diverse plant communities: a sense of moral obligation to living things, an aesthetic appreciation of nature, economic benefits possible from them (e.g., the gene pool for cultivated crops), and the important array of services they provide (e.g., maintaining oxygen levels and cycling nutrients).

A major cause of rangeland deterioration is selective grazing of preferred plants and sites in similar patterns each year (Hormay 1970). Even with conservative grazing, populations of preferred plants on preferred sites may disappear, thereby reducing the overall diversity of vegetation. If such populations are ecotypes (Odum 1959), the ability of the species to recapture site resources is reduced.

Because nature abhors a vacuum, other species may increase or invade as those preferred by livestock decrease in abundance (Dyksterhuis 1949). As a result, plant species diversity may be higher rather than lower under grazing, at least initially. As preferred species decrease and less preferred ones increase, their abundances tend to become more even (Dyksterhuis 1949). With continued deterioration, species not previously able to compete tend to invade and become established and thereby increase species richness. The new plant community, though possibly comprising more species that are more evenly abundant, may cover less total area, and higher diversity may be associated with greater amounts of bare soil.

Increasingly, land managers are asked to monitor and determine change in diversity. Monitoring diversity usually starts with an estimation of alpha diversity for plant communities on specific sites. Such estimates are rare for rangelands. To derive the greatest benefit from monitoring efforts, managers must know what constitutes high and low diversity in given situations. They need to know how diversity changes when other commonly estimated properties of the site change (e.g., litter cover and amount of bare soil).

Seldom will examples of pristine or climax plant communities be available for developing diversity guides. Current plant communities represent the sums of all past influences. Current vegetation and site characteristics, therefore, must serve as benchmarks from which to develop guides and evaluate future change.

The objectives of this study were (1) to provide local rangeland managers with indices of alpha diversity from plant communities to use as guides of expected diversity for similar sites, and (2) to question whether variation in basal cover percentages of common and important indicators of rangeland health could explain variation in diversity. Although the findings are specific to the study area, it is hoped they may assist others dealing with questions of plant species diversity on rangelands.

METHODS

Study Plots

During 1964 and 1965, 51 plots were established on the Harvey Valley and neighboring grazing allotments of the Lassen National Forest, CA (Ratliff et al. 1972). The plots were either 0.1 ha or 0.2 ha and unevenly distributed among meadow (8), open grassland (13), open shrub-grass (12), and timber-bunchgrass (18) vegetation types. These plots were used for evaluating range condition (health) at Harvey Valley relative to the neighboring allotments.

Meadows ranged from ephemeral lake sites with hardpans to deep, organically rich soil of drainage bottoms. Open grasslands included those dominated by shorthair sedge (*Carex exserta*) and those where shorthair sedge had been replaced by grasses. Open shrub-grass areas included silver sagebrush (*Artemisia cana*), black sagebrush (*A. arbuscula*), big sagebrush (*A. tridentata*), and bitterbrush (*Purshia tridentata*) subtypes. The timber-bunchgrass types were all in second-growth ponderosa pine (*Pinus ponderosa*). Some of them had bitterbrush and big sagebrush along with grasses in the understory.

Data Collection

Data used to estimate alpha diversity on each plot were actual point contacts (hits) with plant bases or soil surface components (gravel, litter, rock, bare soil, and large woody debris) and shrub crown area. A hit on a shrub was recorded when a point contacted the shrub crown or was within its projected crown area at the soil surface. For each plot 3060 hits were recorded, consisting of 102 points (in regularly spaced 3-point quadrats) on each of 30 randomly placed transects. Points in a quadrat were at 23-cm centers and projected vertically. Within transects, quadrat spacing was either 0.6 m or 0.9 m, depending upon plot width. Basal cover percentages (proportions of the surface occupied by different plants and surface components) were calculated from the hits and summarized (Ratliff et al. 1972).

Diversity Indices

Two indices of diversity were used: (1) Margalef's $\{D_m = (S - 1)/\ln N\}$, where S is the number of species and N is the total number of individuals (hits) for all species and (2) Simpson's

$(D_s = 1/D)$, where $D = \sum_{i=1}^{S} \{n_i(n_i - 1)/N(N - 1)\}$ and n_i is the number of individuals (here the percentage cover) of the *i*th species (Magurran 1988). D_m was selected for its simplicity and because it stresses the species richness component. D_s was selected because it is well known and stresses the species evenness (dominance) component. In addition, these indices were selected because they do not require testing assumptions regarding the underlying distributions of species abundance.

An overall estimate of diversity was computed for each plot using each index. Then 30 new diversity estimates were computed using the jackknife procedure. This procedure consisted of deleting each transect in turn from the data set. From each new estimate and the overall estimate, a pseudovalue (related form) was computed. From the pseudovalues, means and standard errors for the two indices were derived for each plot. Use of the jackknife procedure to improve estimates of diversity and provide a way of calculating confidence intervals was suggested by Magurran (1988).

Basal Cover Relationships

Contributions of basal cover of various characteristics to the variance in estimates of alpha diversity were examined. Characteristics for each plot were basal covers of grasses, grasslike herbaceous plants, forbs, shrubs, and soil surface components. All possible subset regressions of D_m and D_s on the characteristics were computed using the Mallow's-Cp criterion of the REG procedure (a multiple linear regression program) of the SAS Institute, Inc. (1982). Subset regression models explaining most variation in the indices were selected for study. The Pearson correlation matrix was computed, using the correlations (CORR) module of SYSTAT (Wilkinson 1989), to help assess the influence of individual characteristics on the indices.

RESULTS

Alpha Diversity Indices

Diversity indices and basal cover values are available for all 51 plots. Here, only those plots within each vegetation type ranking lowest

TABLE 1. Numbers of species, dominant species and percentage composition, and jackknifed means and standard errors (SE) for Margalef's and Simpson's diversity indices[1] for vegetation type[2] benchmarks in 1964–65, Eagle Lake Ranger District, Lassen National Forest, CA.

		Dominant		Diversity index			
				Margalef's		Simpson's	
Veg. type	No. of species	Species	Composition percentage	Mean	SE	Mean	SE
MD	6	*Eleocharis palustris*	52	**1.0**	0.2	2.8	0.2
	19	*Deschampsia caespitosa*	62	**4.0**	0.4	**2.4**	0.2
	14	*Juncus balticus*	16	2.3	0.2	**9.9**	0.7
GR	9	*Carex exserta*	71	**1.6**	0.2	1.9	0.1
	9	*C. exserta*	78	1.6	0.2	**1.6**	0.1
	19	*C. exserta*	46	**3.2**	0.3	3.8	0.3
	11	*Festuca idahoensis*	26	2.0	0.3	**5.8**	0.3
SG	5	*Artemisia tridentata*	97	**0.8**	0.2	**1.0**	0.0
	17	*A. arbuscula*	60	**3.6**	0.5	2.6	0.4
	11	*Leptodactylon pungens*	34	1.9	0.3	**5.0**	0.3
TB	7	*Purshia tridentata*	84	**0.8**	0.0	**1.4**	0.1
	13	*Artemisia tridentata*	72	**3.2**	0.4	1.8	0.2
	6	*Carex rossii*	28	1.1	0.2	**4.7**	0.4

[1] Highlighted values are the highest and lowest for each index within vegetation types.

[2] Vegetation types follow Ratliff et al. (1972): MD = meadow, GR = open grassland, SG = open shrub-grass, TB = timber-bunchgrass.

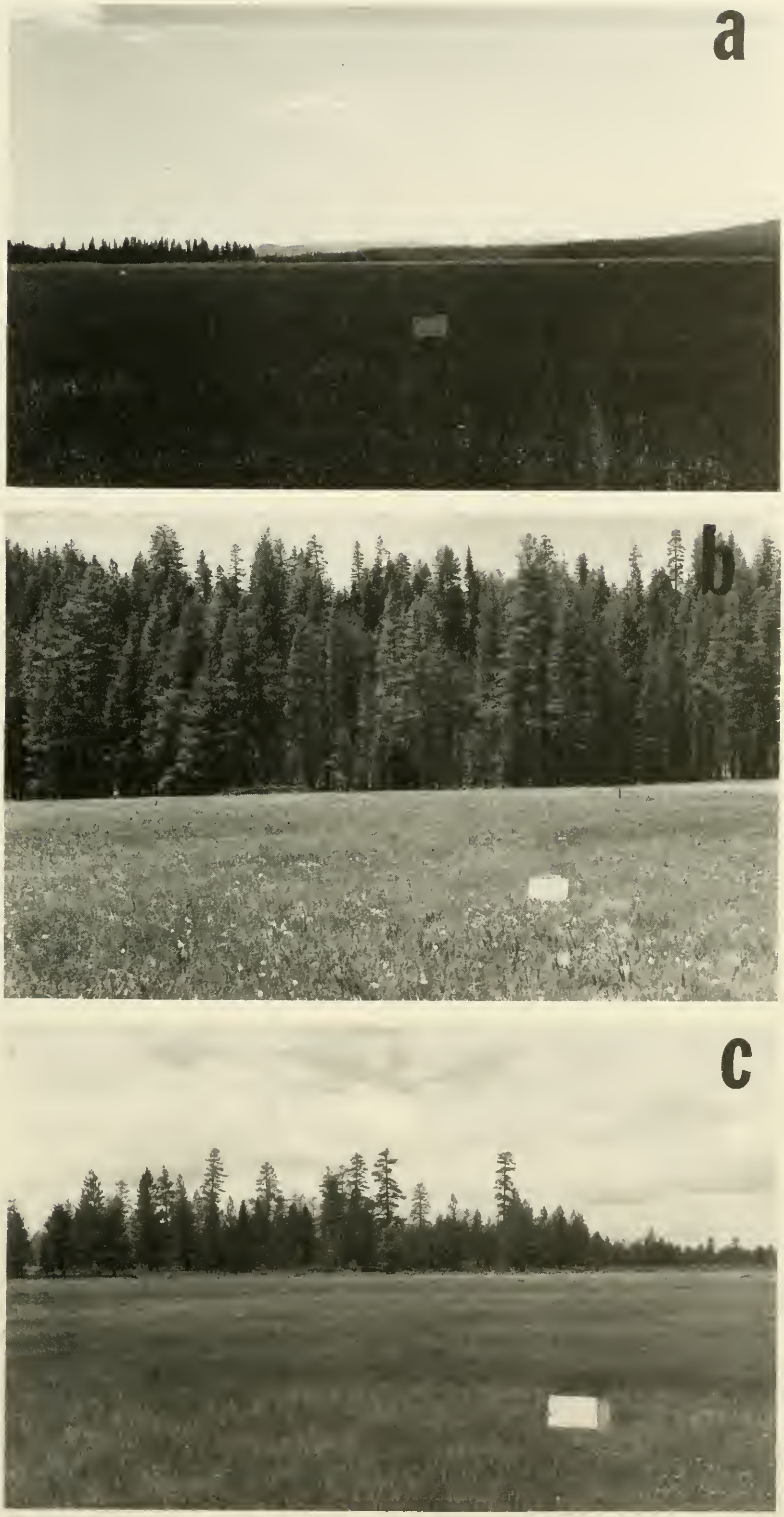

Fig. 1. Meadow diversity benchmarks: (a) *Eleocharis palustris*–, (b) *Deschampsia caespitosa*–, and (c) *Juncus balticus* –dominated plots; Eagle Lake Ranger District, Lassen National Forest, CA.

and highest for D_m and D_s are specifically discussed. Those plots are considered diversity benchmarks for their vegetation types in and near the Harvey Valley allotment.

MEADOW.—D_m in the meadows was lowest on a plot with just six species and demonstrated the effect of lack of richness (Table 1). The site was an ephemeral lake meadow (Fig. 1a) where dominant species covered 3.3% of the surface. Among the meadow plots, percentage litter cover was lowest and percentage bare soil was highest (Table 2).

D_m was highest, but D_s was lowest on a meadow with 19 species. That finding demonstrated the effect of good variety with uneven abundance. The site was a basin meadow, possibly an ancient lake (Fig. 1b). There the dominant species covered 5.7% of the surface. Only one species, among the others, contributed as much as 5% to the composition. Percentages of litter and bare soil were higher and lower, respectively, than averages for the meadow plots (Table 3).

D_s was highest on a plot with 14 species. The site was a groundwater-fed meadow (Fig. 1c). Evenness in species abundance with moderate variety was demonstrated. Four species (including the dominant) each constituted more than 10% of the composition but less than 1% of the basal cover. Only one species, among the others, contributed less than 1% to the composition. Total live plant cover was below average, but percentages of litter and soil cover were well above and below the averages, respectively.

GRASSLAND.—Both D_m and D_s were lowest on grassland plots, with nine species (Figs. 2a, 2b), respectively. Shorthair sedge was the main contributor to the composition. In the case of D_m, three species each contributed 5% or more, and five species each contributed 1% or less. In the case of D_s, only one species, other than shorthair sedge, contributed as much as 5% of the composition. For the plot with low D_m the evenness component was better, litter cover was higher, and bare soil cover was lower than for the plot with low D_s.

D_m was highest on a plot with 19 species (Fig. 2c). Shorthair sedge, Idaho fescue (*Festuca idahoensis*, 20%), and Sandberg bluegrass (*Poa sandbergii*, 9%) were main contributors to the composition. Sixteen species contributed less than 5% each. Among the grassland plots, this plot had the highest live plant cover and was well above average in litter cover and well below average in percentage of bare soil.

Idaho fescue dominated the plot with highest D_s (Fig. 2d). Four of the other 10 species present each made up more than 10% of the composition; two species each made up about 6%. While the evenness component of diversity was good and total live plant cover was

TABLE 2. Percentages of basal cover for plant groups and surface components for vegetation type benchmarks in 1964–65, Eagle Lake Ranger District, Lassen National Forest, CA.

	Percentage basal cover										
	Plant groups[1]						Surface components[2]				
Vegetation type[3]	gr	gl	bl	sh	dp	lp	Gr	Li	Ro	So	Wo
Meadow	1.1	4.6	0.6	—	t[4]	6.2	—	47.1	—	46.6	—
	6.1	2.2	0.9	—	0.7	9.2	0.1	80.2	—	9.8	—
	1.3	2.6	1.2	—	—	5.1	—	90.3	0.1	4.5	—
Open grassland	1.5	5.4	0.5	0.2	15.0	7.6	3.2	57.1	—	17.1	—
	0.7	4.7	0.4	0.2	12.0	6.0	6.0	50.6	0.5	24.9	—
	4.8	5.3	0.6	0.3	7.6	11.1	1.3	60.1	t	19.9	t
	4.4	2.5	0.3	3.0	1.7	10.2	11.3	26.1	2.6	48.1	—
Open shrub-grass	0.7	—	—	25.4	16.2	26.1	18.9	28.4	—	10.4	—
	1.8	0.5	0.8	4.6	8.2	7.6	4.0	38.0	t	42.1	—
	3.6	3.4	1.1	4.5	3.1	12.5	8.6	21.0	1.2	53.7	—
Timber-bunchgrass	1.2	0.6	—	21.6	11.8	23.3	1.2	54.0	0.5	6.5	2.7
	1.0	0.4	0.1	4.5	5.6	5.9	2.9	76.2	4.0	4.6	0.7
	1.0	0.6	—	0.6	3.1	2.1	2.8	62.3	9.4	13.8	6.6

[1] gr = grasses, gl = grasslike herbaceous plants, bl = broadleaf herbaceous plants (forbs), sh = shrubs, dp = dead attached cover, lp = live plant cover (gr + gl + bl + sh).

[2] Gr = gravel, Li = litter, Ro = rock, So = soil, Wo = large woody debris.

[3] Types follow Ratliff et al. (1972), and plot order is the same as in Table 1.

[4] t = less than 0.1% of basal cover.

TABLE 3. Average diversity indices and percentages of basal cover for plant groups, and surface components by vegetation type. Eagle Lake Ranger District, Lassen National Forest, CA, 1964–65.

	Diversity index[1]		Percentage basal cover										
			Plant groups[2]						Surface components[3]				
Vegetation type	D_m	D_s	gr	gl	bl	sh	dp	lp	Gr	Li	Ro	So	Wo
Meadow	2.29	4.38	2.1	3.6	0.8	—	0.3	6.4	0.2	77.2	0.1	15.8	—
Grassland	2.28	3.63	3.3	3.6	1.2	0.8	5.6	8.9	9.3	39.0	1.5	35.7	t
Open shrub-grass	2.28	2.78	1.6	1.3	0.6	14.4	10.7	18.0	7.2	30.2	0.2	33.8	—
Timber-bunchgrass	1.75	2.39	1.1	1.1	0.1	7.7	4.0	10.0	2.5	60.2	3.0	16.4	3.9

[1] D_m = Margalef's index, D_s = Simpson's index.

[2] gr = grasses, gl = grasslike herbaceous plants, bl = broadleaf herbaceous plants (forbs), sh = shrubs, dp = dead attached cover, lp = live plant cover (gr + gl + bl + sh).

[3] Gr = gravel, Li = litter, Ro = rock, So = soil, Wo = wood.

above average, Idaho fescue covered only 3% of the surface and litter cover was well below but bare soil was well above average.

SHRUB-GRASS.—Both indices were lowest on an open shrub-grass plot where big sagebrush contributed over 95% of the composition (Fig. 3a). Only one other species, bottlebrush squirreltail (*Sitanion hystrix*), made up as much as 1%, and only five species occurred on that plot. This finding demonstrates the effects of both low variety and low evenness on diversity. Among the shrub-grass plots, this plot was second highest in total live plant cover (nearly all sagebrush), highest in gravel cover, and lowest in bare soil. This suggests soil loss and formation of pavement.

Black sagebrush dominated the plot with highest D_m (Fig. 3b). Of the 17 species on that plot, 12 of them each contributed less than 3% of the composition. The plot was above average in both litter and soil cover, but lowest in total live plant cover.

The plot with highest D_s (Fig. 3c) had just 11 species and was dominated by false phlox (*Leptodactylon pungens*). Five other species combined contributed nearly 62% of the composition. Among the shrub-grass plots, this plot was well below average in litter cover but highest in bare soil.

TIMBER-BUNCHGRASS.—Both indices were lowest (Fig. 4a) on a timber-bunchgrass plot with seven species. Bitterbrush contributed over 80% of the composition. Three species contributed 2% or more and three species contributed less than 1% of the composition. While total live plant cover was above average, litter was near average and bare soil was well below average; there were few species, and they were unevenly abundant. This plot was similar in diversity to the shrub-grass plot with D_m and D_s both low.

D_m was highest on a plot with 13 species (Fig. 4b). Nine of them contributed 1% or less of the composition, thereby demonstrating that high evenness is not required when variety is the main component of diversity considered. Big sagebrush dominated the understory and covered 4.3% of the surface. Litter cover was well above and bare soil was well below average for the timber-bunchgrass plots.

By contrast, D_s was highest on a plot with just six species (Fig. 4c). Ross sedge (*Carex rossii*) contributed most of the composition (0.6% of the surface cover), three species contributed 15–26% each, and two species contributed 3% each, thereby demonstrating that high variety is not required when evenness is the main component of diversity considered. Percentages of soil and litter cover were near average for the timber-bunchgrass plots.

Beta Diversity Indices

Statistical comparisons of diversity among communities and vegetation types were not made. Nevertheless, average values for both indices declined from meadow to grassland to open shrub-grass to timber-bunchgrass types (Table 3).

Relative plot ranking (high to low diversity) depends on the index used, and inconsistent ranking by D_m and D_s was expected. Among the open shrub-grass and timber-bunchgrass types only two plots ranked the same, those with lowest diversity by both indices. Rankings by D_m and D_s were the same for 3 of the 8 meadow plots and 2 of the 13 open grassland plots.

Basal Cover Relationships

Meadow and grassland plots had higher average diversity indices than open shrub-grass

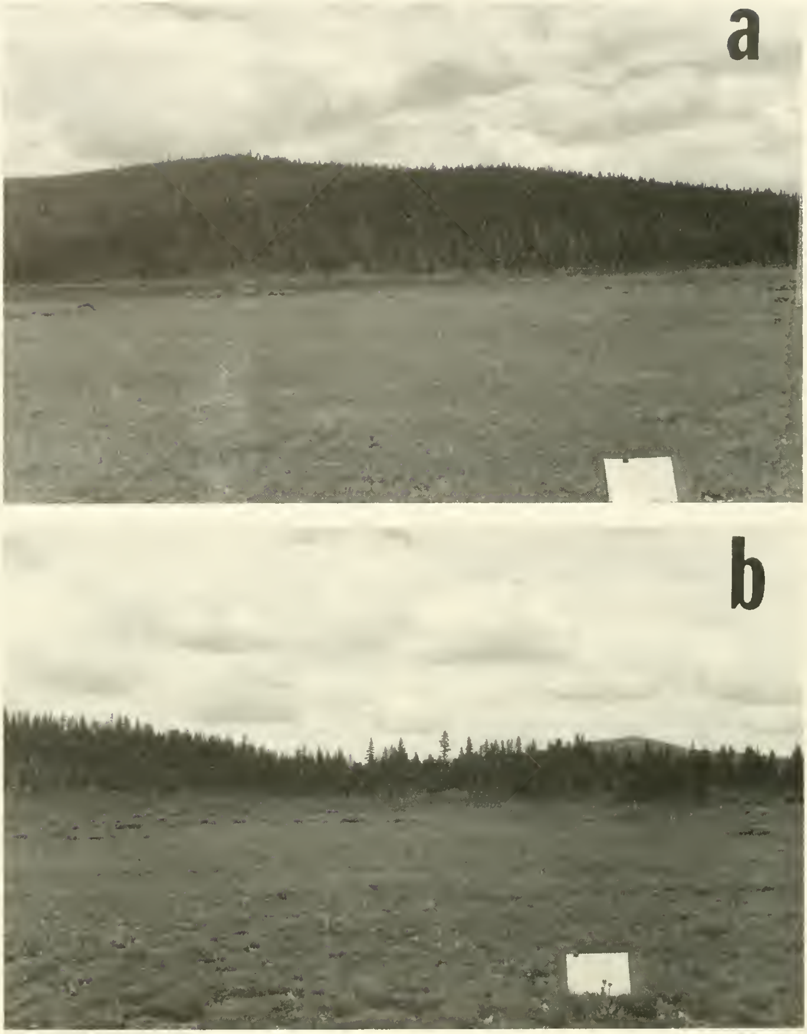

Fig. 2. Open grassland diversity benchmarks: (a, b, c) *Carex exserta*– and (d) *Festuca idahoensis*–dominated plots; Eagle Lake Ranger District, Lassen National Forest, CA.

or timber-bunchgrass plots, but lower average percentages of live plant cover (Table 3). Total live plant cover was largely a property of shrub cover because projected crown hits were incorporated into the data base.

Significant portions of variances in the diversity indices (all 51 plots included) were accounted for by variation in percentages of some basal cover characteristics. Forty-seven percent of the variation in D_m and 27% of the variation in D_s were explained by the best models (Table 4).

$D_m = a + grb_1 + glb_2 + shb_3 + Grb_4 + Sob_5 + Wob_6 + error$) and $D_s = a + shb_1 + Grb_2 + error$, where a, gr, gl, sh, Gr, So, and Wo are explained in Table 4; and the (b_i)'s are the coefficients.

Although gravel and bare soil were included in the model for D_m, they did not significantly correlate with D_m. Also, while in the model for D_s, gravel was not significantly correlated with D_s.

Individually, correlation with D_m was positive for grasses ($r = .471$) but negative for grass-like plants ($r = -.014$), shrubs ($r = -.320$), and wood ($r = -.348$). Correlation of D_s with shrubs was negative ($r = -.507$), also.

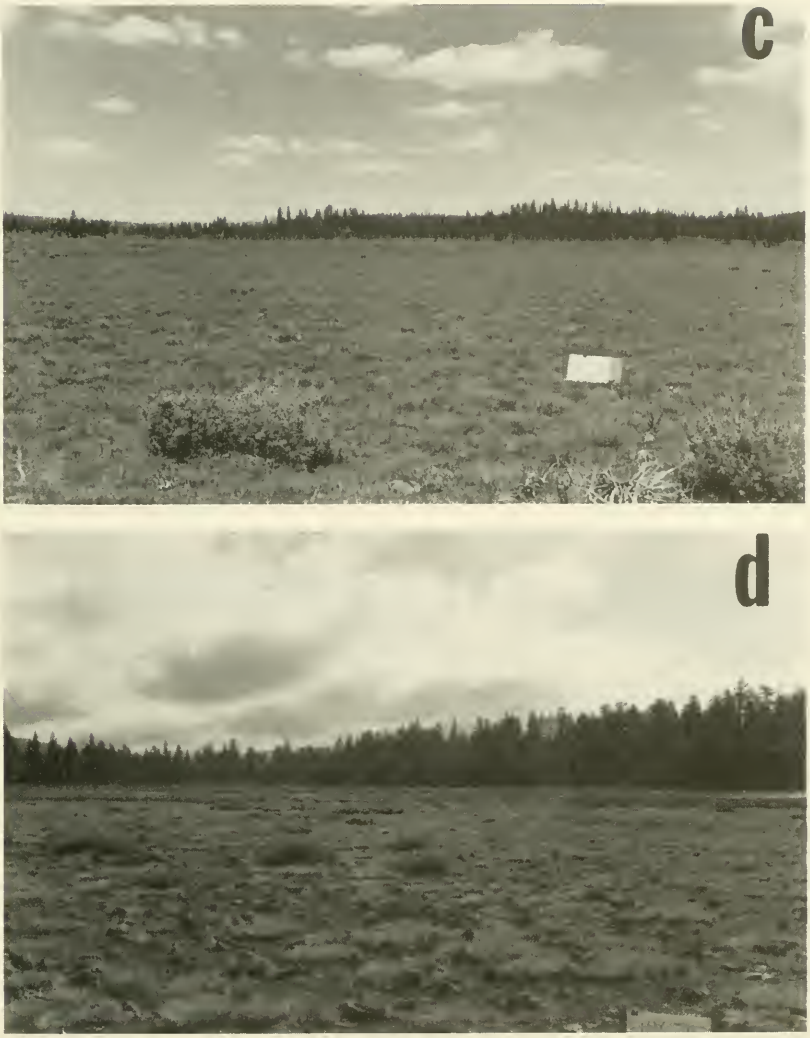

Fig. 2. Continued.

DISCUSSION

Alpha Diversity

Many diversity indices are available to the land manager. Although a particular diversity index may be preferred, it is generally best to use one that stresses species richness and one that stresses evenness (dominance), such as D_m and D_s, respectively. Doing so allows the manager to consider both components of diversity. The richness component of diversity may increase at the expense of the evenness component, or vice versa. Also, those indices that stress richness and those that stress evenness tend to be poorly correlated (Magurran 1988).

Beta Diversity

Data used in this study represent single-time samples and were not designed to estimate beta diversity. Testing for differences in diversity using such data was not considered reliable (West and Reese 1991).

Nevertheless, diversity indices for different but closely similar plots or communities, when computed by the same methods, should be nearly equal. With time or different treatment, wide divergence of the indices may occur.

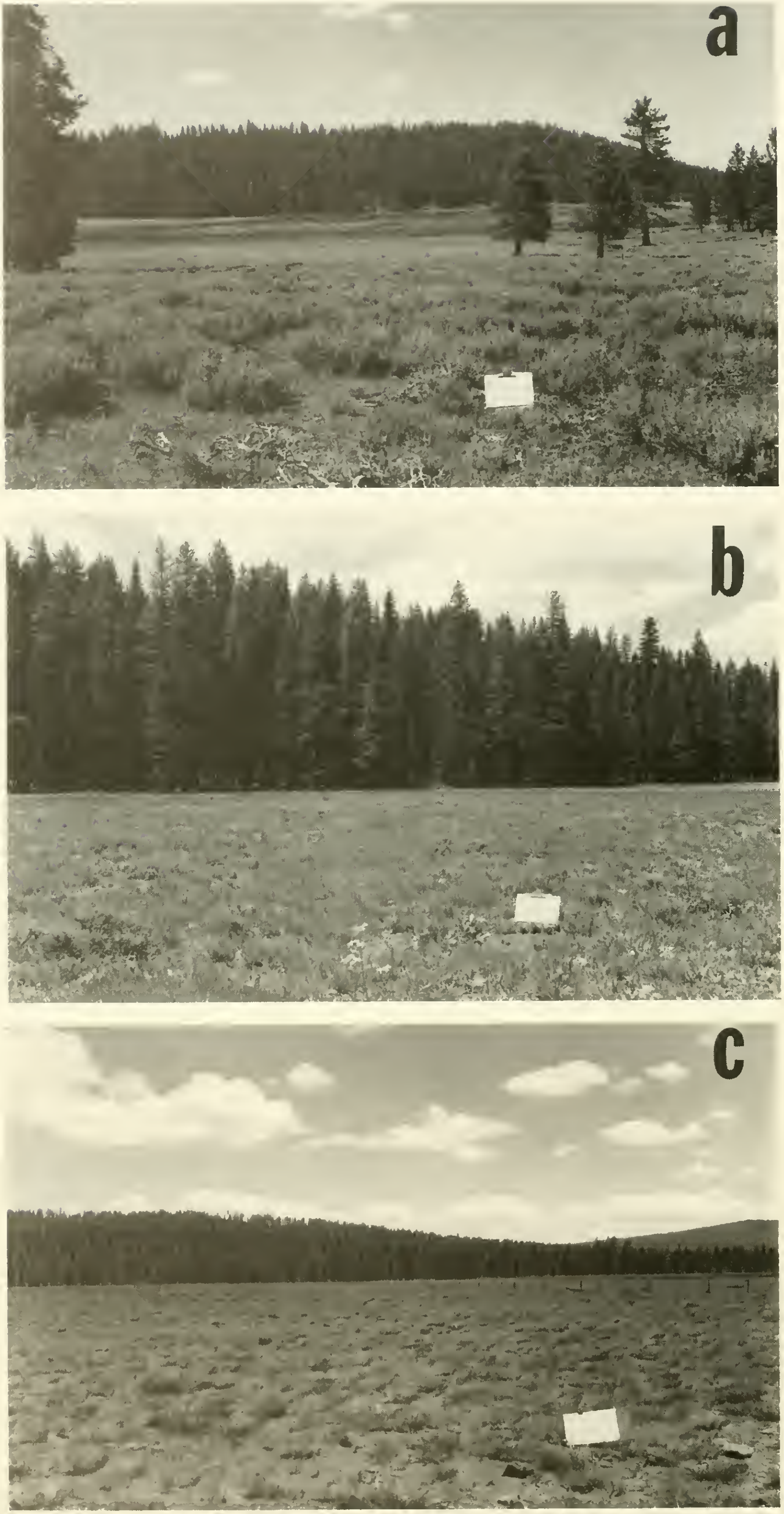

Fig. 3. Open shrub-grass diversity benchmarks: (a) *Artemisia tridentata*–, (b) *A. arbuscula*–, and (c) *Leptodactylon pungens*–dominated plots; Eagle Lake Ranger District, Lassen National Forest, CA.

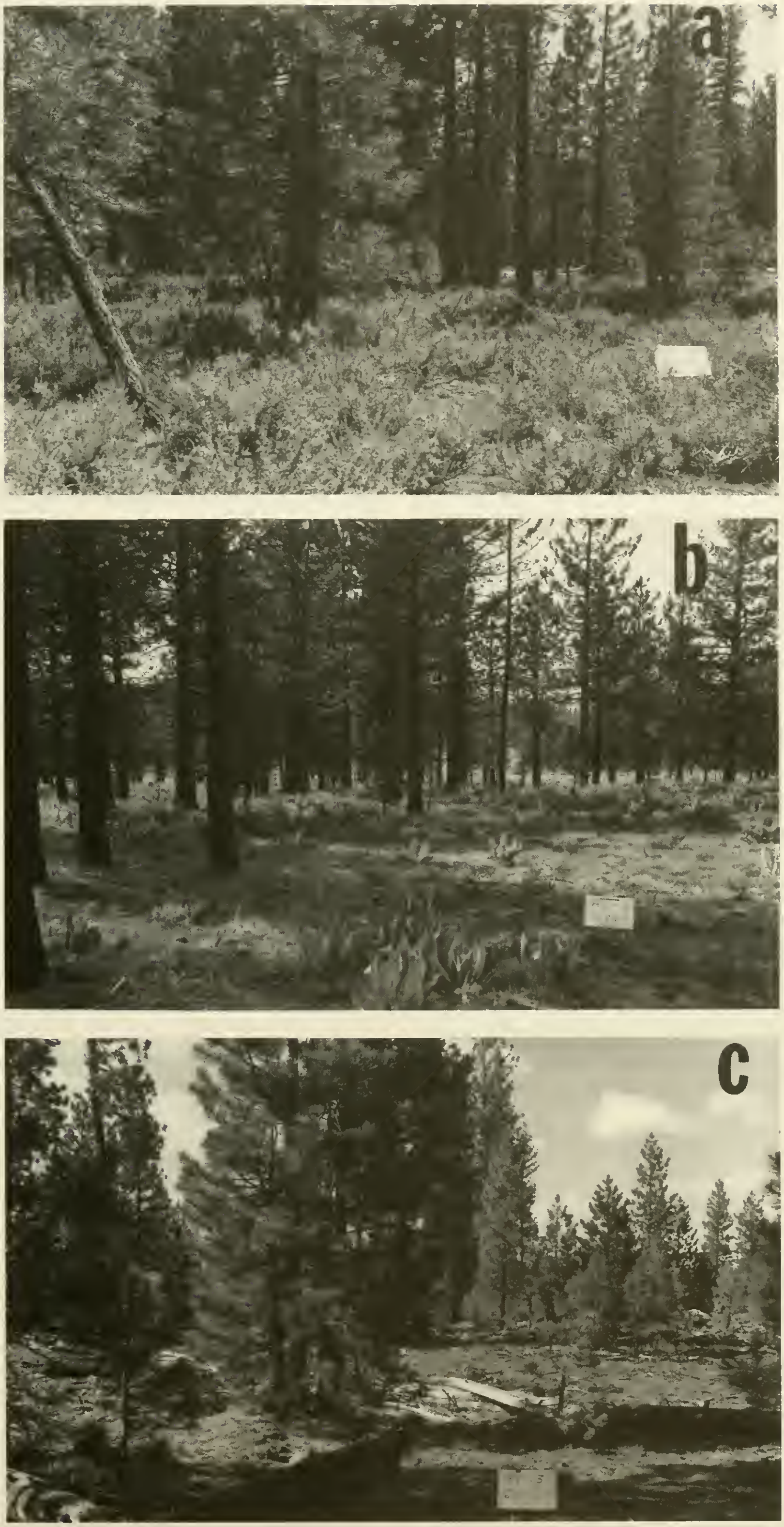

Fig. 4. Timber-bunchgrass diversity benchmarks: (a) *Purshia tridentata*–, (b) *Artemisia tridentata*–, and (c) *Carex rossii* –dominated plots; Eagle Lake Ranger District, Lassen National Forest, CA.

TABLE 4. Best model multiple linear regression coefficients, tests of significance (T), and probabilities of significance (*P*) for Margalef's and Simpson's diversity indices; Eagle Lake Ranger District, Lassen National Forest, CA, 1964–65.

		Diversity index					
		Margalef's			Simpson's		
Variable	Symbol	Coeff.[1]	T	*P*	Coeff.	T	*P*
Constant	a	2.696	8.436	.000	3.584	12.372	.000
Grasses	gr	0.238	3.522	.001			
Grasslike plants	gl	–0.161	–3.285	.002			
Shrubs	sh	–0.036	–2.722	.009	–0.102	–4.194	.000
Gravel	Gr	–0.026	–1.505	.139	0.033	0.970	.337
Bare soil	So	–0.007	–1.197	.238			
Wood	Wo	–0.128	–3.173	.003			

[1] Regression coefficient

Permanent plots represent a resource for assessing beta diversity responses to land management practices. Although sampling a site to include within- and between-season variation is desirable, doing so is seldom possible, given time and monetary constraints. As an alternative, one might restrict sampling to times when selected species indicators are in specific phenologic stages (e.g., budding or flowering).

Basal Cover

Because of the usual dominance of a single species and because that species tends to occupy high proportions of an area, reductions in diversity indices with increases in shrub cover may be expected.

Both diversity indices may be related positively or negatively to characteristics of basal cover or to soil properties. Nevertheless, D_m was related to a greater number of characteristics than D_s, suggesting that D_m may be the more desirable index for comparing plant communities of different sites or plant communities present through time on a given site.

CONCLUSIONS

For similar communities we can expect plant species diversity to be highest in the meadow and lowest in the pine-bunchgrass types. High and low values of Margalef's and Simpson's diversity indices are available for benchmark plots of different vegetation types in and near the Harvey Valley allotment. Diversity indices for and averages among 51 plots are available by vegetation types.

The influence of species richness on D_m was clearly evident. D_m tended to be highest with the greatest numbers of species. Frequently that occurred when one species was clearly dominant and the others contributed little plant cover. The influence of evenness in abundance on D_s was clearly evident. D_s tended to be highest when species were more or less evenly abundant. Frequently that occurred with relatively few species. Few species with one contributing a high percentage of the composition produced low values of both indices. Situations with many species, all contributing equally to the composition, were not encountered, but such situations should give high values of D_m and D_s.

Higher diversity did not necessarily mean greater plant cover or greater forage cover or more litter or less bare soil. While some relationships between diversity and basal cover values were significant, coefficients of determination were too low to allow either of the best models to be used to predict diversity.

Neither index should be relied on apart from other information for evaluating rangeland health. Nevertheless, plants capture the sun's energy and pass it as food for other organisms, and a high degree of plant diversity may equate with high diversity in other parts of the biotic community.

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EFFECTS OF SALINITY ON ESTABLISHMENT OF *POPULUS FREMONTII* (COTTONWOOD) AND *TAMARIX RAMOSISSIMA* (SALTCEDAR) IN SOUTHWESTERN UNITED STATES

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ABSTRACT.—The exotic shrub *Tamarix ramosissima* (saltcedar) has replaced the native *Populus fremontii* (cottonwood) along many streams in southwestern United States. We used a controlled outdoor experiment to examine the influence of river salinity on germination and first-year survival of *P. fremontii* var. *wislizenii* (Rio Grande cottonwood) and *T. ramosissima* on freshly deposited alluvial bars. We grew both species from seed in planters of sand subjected to a declining water table and solutions containing 0, 1, 3, and 5 times the concentrations of major ions in the Rio Grande at San Marcial, NM (1.2, 10.0, 25.7, and 37.4 meq l^{-1}; 0.11, 0.97, 2.37, and 3.45 dS m^{-1}). Germination of *P. fremontii* declined by 35% with increasing salinity ($P = .008$). Germination of *T. ramosissima* was not affected. There were no significant effects of salinity on mortality or above- and belowground growth of either species. In laboratory tests the same salinities had no effect on *P. fremontii* germination. *P. fremontii* germination is more sensitive to salinity outdoors than in covered petri dishes, probably because water scarcity resulting from evaporation intensifies the low soil water potentials associated with high salinity. River salinity appears to play only a minor role in determining relative numbers of *P. fremontii* and *T. ramosissima* seedlings on freshly deposited sandbars. However, over many years salt becomes concentrated on floodplains as a result of evaporation and salt extrusion from saltcedar leaves. *T. ramosissima* is known to be more tolerant of the resulting extreme salinities than *P. fremontii*. Therefore, increases in river salinities could indirectly contribute to decline of *P. fremontii* forests by exacerbating salt accumulation on floodplains.

Key words: exotic species, Tamarix ramosissima, Populus fremontii, *river salinity, seedling establishment, Rio Grande, riparian vegetation, Bosque del Apache National Wildlife Refuge.*

In the last century the exotic shrub saltcedar (*Tamarix ramosissima* Ledebour) has spread throughout southwestern United States, where it now dominates many riparian ecosystems (Bowser 1958, Robinson 1965). In many areas *T. ramosissima* has replaced stands dominated by the native Fremont cottonwood (*Populus fremontii* Wats.; Campbell and Dick-Peddie 1964, Ohmart et al. 1977), decreasing the habitat of Neotropical migrant birds (Anderson et al. 1977, Cohan et al. 1978) and altering fluvial processes (Graf 1978, Blackburn et al. 1982). Understanding the factors controlling establishment of *T. ramosissima* and *P. fremontii* can aid in managing these species.

Successful invasion by *Tamarix* in the Southwest has been attributed to many factors. Much of the early spread probably resulted from the coincidental timing of clearing of *P. fremontii* stands by early settlers and the availability of *Tamarix* seed (Campbell and Dick-Peddie 1964, Harris 1966, Horton and Campbell 1974, Ohmart et al. 1977). Subsequent spread resulted largely from effects of damming and channelizing southwestern watercourses. Reductions in the magnitude of high flows and associated reductions in channel movements decreased the formation of bare, moist alluvial bars, which provide ideal *P. fremontii* seedling habitat (Ohmart et al. 1977, Stromberg et al. 1991). Smaller peak flows have also reduced leaching of salts from floodplain soils (Busch and Smith in press), perhaps favoring the salt-tolerant *Tamarix* (Everitt 1980, Brotherson and Winkel 1986, Jackson et al. 1990). Flow regulations that have altered the historical timing of peak flows may have inhibited *P. fremontii* regeneration because of its short period of seed dispersal and viability in early summer (Horton 1977, Everitt 1980), but they have enhanced *Tamarix* regeneration because of its abundant seed production throughout the growing season (Merkel and Hopkins 1957, Tomanek and Ziegler 1962, Warren and Turner 1975, Horton 1977). Finally, successful invasion of *T. ramosissima* has been attributed to its superior ability to resprout following fire (Busch and Smith 1993).

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We conducted experiments to examine the influence of river salinity on germination, survival, and growth of *Populus fremontii* var. *wislizenii* (Rio Grande cottonwood) and *T. ramosissima* on freshly deposited alluvial bars, the principal habitat for seedling establishment of both species. Field observations have suggested that *P. fremontii* is more negatively affected by high salt concentrations than *T. ramosissima* (Brotherson and Winkel 1986, Anderson 1989). Laboratory studies have confirmed this difference by exposing seedlings and cuttings of these species to varying concentrations of NaCl and $CaCl_2$ (Jackson et al. 1990, Siegel and Brock 1990). Two factors potentially confound the relationship of results of laboratory studies to field conditions. First, the mix of salts found in riparian ecosystems typically includes many constituents other than Na, Ca, and Cl. In many plants, salinity effects result from toxicity of specific ions as opposed to osmotic stress (Greenway and Munns 1980). Second, moisture availability is lower and more variable in the field than in these laboratory studies. This factor is important because low soil water potential caused by high salinity is exacerbated by low soil moisture content. We addressed these concerns by exposing *T. ramosissima* and *P. fremontii* seedlings to four different concentrations of a mix of salts designed to mimic ion concentrations in the Rio Grande. The experiment was conducted outdoors in planters subjected to a controlled water-table drawdown. Experimental conditions were designed to simulate alluvial bars along the Rio Grande in central New Mexico, where once-extensive *P. fremontii* forests have largely been replaced by *T. ramosissima* thickets (Campbell and Dick-Peddie 1964). Our outdoor experiments were supplemented by studies of germination under similar salinity treatments in the laboratory.

METHODS

Seedling establishment experiments were conducted outdoors in 1993 near Fort Collins, CO, at latitude 40°35′ north, longitude 105°5′ west, and elevation 1524 m. Twelve 122 × 92-cm (diameter × depth) epoxy-lined steel tanks contained six 30 × 100-cm planters made of PVC pipe. Holes 1.26 cm in diameter were drilled into the lower 10 cm of each planter to allow water exchange, and the planters were filled to 92 cm with washed coarse sand (approximately 6% gravel [>2000 μm], 78% sand [>300–2000 μm], 16% fine sand [>75–300 μm], and <1% silt and clay).

Four salinity treatments were each replicated in three tanks (12 tanks total). Each tank contained three planters of *P. fremontii* var. *wislizenii* and three of *T. ramosissima*. Thus, the experimental unit for each species was a group of three planters within a tank. To avoid pseudoreplication, responses were measured as the mean value of the three planters. The results for the two species were analyzed as separate, completely randomized experiments with four treatments and three replicates per treatment.

The tanks were filled with water from the Cache la Poudre River (a snowmelt stream low in dissolved solids), and solutions containing multiples (0, 1, 3, and 5 times) of the mean concentration of all major ions in the middle Rio Grande were made. These four solutions constitute treatments 0x, 1x, 3x, and 5x. Mean ion concentrations were derived from eight measurements from the conveyance channel at San Marcial, NM, between October 1989 and September 1991 (U.S. Geological Survey 1991, 1992). The following salts were added to make treatment 1x: 309.9 mg l^{-1} $CaSO_4{*}2H_2O$; 302.4 mg l^{-1} $NaHCO_3$; 122.0 mg l^{-1} $MgCl_2{*}6H_2O$; 70.1 mg l^{-1} NaCl; 13.9 mg l^{-1} K_2SO_4. Because the coarse sand substrate was low in nutrients (cf. Segelquist et al. 1993), 15 mg l^{-1} of Fisons Technigro fertilizer (16% N, 17% P, 17% K) was added to every tank.

At the time of planting and for 1 wk thereafter, the water level was 10 cm below the soil surface. A 3.5-cm-week^{-1} drawdown rate was applied for the remainder of the growing season (17 June to late September). Water-table drawdowns are associated with summer declines in discharge along western streams. The 3.5-cm-week^{-1} drawdown rate was selected because a previous study (Segelquist et al. 1993) indicated that it is within the optimal range for establishment and growth of plains cottonwood (*Populus deltoides* ssp. *monilifera*).

Flowering panicles of *T. ramosissima* were collected on 17 May at the Bosque del Apache National Wildlife Refuge (latitude 33°46′ north, longitude 106°54′ west, elevation 1375 m). The panicles were air-dried for 48 h to enhance opening of seed capsules. Collected material was sifted through a series of soil screens until clean samples of seeds were obtained. Catkins of *P. fremontii* were collected at the Bosque del Apache on 1 June. The catkins were air-dried for 72 h to enhance opening of seed capsules. Capsules were placed between soil screens and seeds were separated from the cotton and capsules using forced air. Seeds of both species were sealed in plastic containers and refrigerated at 5°C (Zasada and Densmore 1977). On 10 June, 100 *P. fremontii* seeds were planted in each of three planters per tank, and 200 *T. ramosissima* seeds were planted in each of the other three planters.

Electrical conductivity (EC) and temperature were measured using a Yellow Springs Instrument Co., Inc., Model 33 S-C-T meter, and pH was measured using a Corning 105 hand-held pH meter in conjunction with a Corning ATC temperature probe and a Corning general purpose combination electrode. EC was measured weekly in every tank begining 12 June (17 measuring dates). Whenever EC was measured, a representative water temperature for that day was determined by averaging the temperature values from five randomly selected tanks. All EC measurements were corrected for temperature and reported at 25°C. Fourteen weekly measurements of pH were made beginning 30 June. On 16 June, 14 July, 18 August, and 17 September, water samples from one randomly selected tank per treatment were analyzed to determine concentrations of Ca, Mg, Na, K, CO_3, HCO_3, Cl, SO_4, and NO_3. Ca, Mg, Na, and K were determined by inductively coupled plasma emission spectroscopy (ICP; EPA method 200.0, United States Environmental Protection Agency 1983); CO_3 and HCO_3 were determined by titration (EPA method 310.1, United States Environmental Protection Agency 1983); Cl, SO_4, and NO_3 were determined by ion chromatography. Concentrations are reported in meq l^{-1} to facilitate comparison of our solutions to solutions in other studies and because meq l^{-1} can be related easily to electrical conductivity, which is commonly reported in the context of salinity studies.

On 29 September 1993 (day 112) we measured the shoot length of every living seedling. We harvested all live seedlings in early October. To harvest, we lifted a planter and laid it horizontally in a water-filled basin. The planter was then slowly lifted upside down, leaving the substrate column and seedlings in the basin. We gently separated seedlings from the sand and water and measured total length of every harvested seedling. Mean root lengths were determined by subtracting the mean shoot length for a planter from the mean total length in that planter. Roots and shoots were separated for both species, and *P. fremontii* leaves were stripped from the stems. Roots, shoots, and leaves were dried at 60°C for 72 h and weighed.

One-way analysis of variance (SAS Institute, Inc. 1990) was used to assess the significance of treatment differences within the two species for five variables: percent of planted seeds alive at the end of the experiment ("end-of-season survival"), shoot length, root length, per-plant aboveground biomass, and per-plant root biomass. For all variables the mean value of the three planters in a tank was the unit of analysis. The arcsine transformation was applied to end-of-season survival values to meet the equal variance assumption (Snedecor and Cochran 1980).

Data from the Colorado Climate Center were used to determine the difference between precipitation and open-pan evaporation (adjusted with pan coefficient = 0.73) for the period 1 June–30 September 1993 in Fort Collins. Evaporation at Fort Collins exceeded precipitation by 26.2 cm during this period. The same calculation was made for the Bosque del Apache using data from the Western Regional Climate Center for the years 1975 through 1990. Precipitation data are from the Bosque del Apache National Wildlife Refuge, and open-pan evaporation data are from Socorro, NM (latitude 34°5′ north, longitude 106°53′ west, elevation 1399 m; pan coefficient = 0.73). Growing-season evaporation at the Bosque del Apache exceeded precipitation by an average of 40.6 cm; $n = 16$, maximum = 51.0 cm, and minimum = 32.3 cm during these 16 years.

We performed laboratory germination experiments in January 1994. Five 25-seed replicates of five salinity treatments were completely randomized for both *T. ramosissima* and *P. fremontii*. Seeds were sowed in 7.5-cm petri dishes containing a Whatman #3 filter and 7 ml of a treatment solution. Petri dishes were placed in a Percival Model I-35 biological incubator after sealing the dish tops with Parafilm. Temperature in the incubator was 20°C throughout the experiment, and petri dishes were exposed to 16 h of light and 8 h of darkness each day. Four of the treatment solutions were the same as those used in the establishment experiment (0, 1, 3, and 5 times the concentration of the Rio Grande at San Marcial, NM); the fifth solution contained 7 times the concentration of the Rio Grande. Germinants in every petri dish were counted after seven days. A seed was considered germinated if it exhibited expanded cotyledons and an elongated radicle. The arcsine transformation was applied to percent germination values to meet the equal variance assumption, and one-way analysis of variance was performed on the transformed values (SAS Institute, Inc. 1990). When germination equaled 100%, the proportion was counted as $(n - 0.25)/n$, where n = the number of seeds planted (Snedecor and Cochran 1980).

RESULTS

EC and pH in the tanks varied little within treatments over the course of the experiment (Table 1). Mean temperature in the tanks was 21.7°C (standard error = 0.8, $n = 17$). Concentrations of measured chemical constituents in different treatments did not increase proportionally to the quantities of salt originally added, indicating that salts (especially $CaCO_3$) precipitated at higher concentrations (Table 1). Nevertheless, concentrations increased across treatments, with total concentrations ranging from 0.7 meq l^{-1} (0.11 dS m^{-1}) in treatment 0x to 37.4 meq l^{-1} (3.45 dS m^{-1}) in treatment 5x (Table 1).

For *P. fremontii* there was a significant treatment effect ($P = .003$) on end-of-season survival, but not on any of the four measured growth variables (Table 2). End-of-season survival was negatively associated with increasing salinity: survival was greatest in treatment 0x and lowest in treatment 5x. Because the end-of-season survival variable combines germination and mortality, we analyzed the arcsine-transformed number of seedlings 7 d after planting (germination), and the arcsine-transformed difference between germination and end-of-

TABLE 1. Chemical analysis of tank water for four treatments in the outdoor establishment experiment in Fort Collins, CO. For ion concentrations ($n = 4$), minimum and maximum values are presented in parentheses below treatment means. For electrical conductivity ($n = 51$) and pH ($n = 42$), means ± 1 standard error are presented.

	Treatment			
Factor	0x	1x	3x	5x
Ca (mmol l^{-1})	0.36	1.82	4.02	4.54
	(0.20, 0.52)	(1.71, 2.00)	(3.49, 4.83)	(3.02, 7.02)
Mg (mmol l^{-1})	0.11	0.60	1.65	2.62
	(0.08, 0.16)	(0.46, 0.75)	(1.47, 1.97)	(2.28, 2.97)
Na (mmol l^{-1})	0.17	4.85	13.87	22.24
	(0.09, 0.28)	(4.41, 5.11)	(11.91, 15.49)	(19.33, 24.65)
K (mmol l^{-1})	0.08	0.26	0.51	0.79
	(0.06, 0.09)	(0.20, 0.34)	(0.44, 0.55)	(0.72, 0.90)
$HC0_3$ (mmol l^{-1})	1.04	3.92	8.34	9.60
	(0.62, 1.44)	(3.24, 4.44)	(7.29, 9.96)	(5.87, 15.74)
Cl (mmol l^{-1})	0.10	2.47	7.10	12.12
	(0.07, 0.14)	(1.88, 2.82)	(6.96, 7.31)	(10.88, 13.21)
$S0_4$ (mmol l^{-1})	0.04	1.66	5.06	7.73
	(0.04, 0.05)	(1.32, 1.86)	(4.76, 5.32)	(7.13, 8.33)
$N0_3$ (mmol l^{-1})	0.03	0.03	0.05	0.06
	(0.002, 0.08)	(0.006, 0.09)	(0.01, 0.08)	(0.02, 0.15)
Total cations (meq l^{-1})	1.2	10.0	25.7	37.4
	(0.7, 1.6)	(9.2, 10.8)	(23.8, 26.7)	(34.5, 41.5)
EC (dS m^{-1})	1.09 ± 0.03	0.97 ± 0.11	2.37 ± 0.23	3.45 ± 0.39
pH	7.54 ± 0.03	8.10 ± 0.02	8.29 ± 0.02	8.05 ± 0.03

TABLE 2. Survival and growth of *Populus fremontii* and *Tamarix ramosissima* seedlings exposed to four different salinity treatments for one growing season outdoors in Fort Collins, CO. High and low replicate means are given in parentheses below the treatment means (n = 3). Treatment effects were analyzed by completely randomized one-way ANOVA. Survival ANOVA was performed on arcsine-transformed data.

Species Variable	Treatment					
	0x	1x	3x	5x	*F*	*P*
Cottonwood						
Survival (% of planted seed)	57.0 (50.0, 63.0)	49.3 (45.7, 54.0)	46.6 (41.0, 51.0)	29.0 (20.7, 35.0)	11.4	.003
Shoot height (mm)	33.9 (32.8, 34.5)	36.3 (34.5, 38.5)	39.6 (36.5, 43.9)	38.3 (34.7, 40.8)	2.6	.13
Root length (mm)	239.2 (227.1, 258.4)	280.9 (257.8, 309.3)	286.9 (253.6, 311.7)	247.4 (206.3, 274.6)	2.1	.17
Per-plant shoot biomass (mg)	14.1 (13.7, 14.4)	14.6 (11.2, 16.6)	21.4 (18.9, 25.8)	19.8 (14.3, 25.9)	2.8	.11
Per-plant root biomass (mg)	26.8 (21.2, 35.5)	19.6 (16.4, 21.3)	31.8 (21.6, 43.2)	31.2 (17.2, 42.9)	1.1	.41
Saltcedar						
Survival (% of planted seed)	42.3 (29.5, 51.6)	37.8 (33.8, 42.0)	37.3 (31.8, 40.8)	29.5 (22.8, 35.2)	1.6	.26
Shoot height (mm)	18.1 (17.3, 18.8)	17.7 (15.5, 19.8)	18.2 (15.6, 22.2)	18.3 (18.2, 18.3)	0.04	.99
Root length (mm)	174.4 (166.4, 184.9)	173.6 (154.8, 192.9)	179.0 (128.1, 243.6)	162.0 (147.2, 169.5)	0.15	.92
Per-plant shoot biomass (mg)	5.5 (4.8, 6.2)	5.5 (4.1, 6.4)	6.3 (4.3, 9.6)	6.2 (5.8, 6.4)	0.22	.88
Per-plant root biomass (mg)	7.7 (7.1, 8.9)	7.3 (5.5, 9.2)	9.9 (7.0, 14.7)	9.5 (7.6, 12.1)	0.74	.56

season survival (mortality). There was a significant treatment effect on germination (P = .008), but not on mortality (P = .45), indicating that the effect on end-of-season survival was predominantly due to lower germination at higher salt concentrations. For *T. ramosissima* there were no significant treatment effects (Table 2).

Although *P. fremontii* germination in outdoor tanks was significantly decreased at high salinity, laboratory germination was not similarly affected even at seven times the salinity of the Rio Grande, total concentration 48.4 meq l^{-1} (4.56 dS m^{-1}; Table 3). There was a significant positive effect of increasing salinity on *T. ramosissima* germination (P = .03) (Table 3).

DISCUSSION

The absence of a negative effect of salinity on *P. fremontii* germination in the laboratory at concentrations as high as 48.4 meq l^{-1} (4.56 dS m^{-1}) is consistent with results of earlier studies. Jackson et al. (1990) found that *P. fremontii* germinated in the laboratory at salinities of 0, 27, and 106 meq l^{-1} using a mixture of NaCl and $CaCl_2$, but not at 319 meq l^{-1} or above. Siegel and Brock (1990) observed higher percent germination of *P. fremontii* in the laboratory in NaCl solutions of 0, 25, and 50 meq l^{-1} than at 100 meq l^{-1} and above. Therefore, *P. fremontii* is no more sensitive to the mix of salts present in the Rio Grande than to NaCl and $CaCl_2$ solutions of equal strength. Tests at higher salinities with the same ionic ratios were not possible with our Rio Grande mix because of low solubilities of some of the constituent salts. The decrease in *T. ramosissima* germination at low salinity in the laboratory (Table 3) is consistent with the finding by Jackson et al. (1990) that germination increases between 0 and 106 meq l^{-1}.

Our results indicate that a given water salinity may negatively affect germination of *P.*

TABLE 3. Percent germination of *Populus fremontii* and *Tamarix ramosissima* seedlings exposed to five salinity treatments in covered petri dishes. High and low replicate values are given below the treatment mean (n = 5). Treatment effects were analyzed by completely randomized one-way ANOVA using arcsine-transformed data.

	Treatment						
Species	0x	1x	3x	5x	7x	*F*	*P*
Cottonwood	90.4 (80.0, 100.0)	96.0 (92.0, 100.0)	96.0 (92.0, 100.0)	92.8 (84.0, 96.0)	96.0 (92.0, 100.0)	1.2	.35
Saltcedar	69.6 (60.0, 88.0)	68.8 (56.0, 80.0)	78.4 (68.0, 92.0)	84.8 (76.0, 92.0)	84.0 (76.0, 92.0)	3.3	.03

fremontii seeds under ambient conditions but not under laboratory conditions. This may have resulted from an interaction between the effects of salinity and soil moisture content, or from vapor-pressure deficit differences. In outdoor planters, but not laboratory petri dishes, evaporation of water may have resulted in lower soil moisture and higher salt concentration at the soil surface. These factors would both tend to reduce soil water potential, thereby increasing plant water stress. Because the difference between evaporation and precipitation is somewhat greater at the Bosque del Apache than in Fort Collins, the effect of salinity might be stronger at the Bosque, especially in dry years. Finally, greater vapor-pressure deficits in the field relative to the laboratory may have exacerbated plant water stress.

Salinity appears to be a relatively minor factor regulating numbers of *P. fremontii* and *T. ramosissima* seedlings on freshly deposited sandbars along the Rio Grande. The only significant effects of increasing salinity were a small decrease in *P. fremontii* germination in outdoor planters and a small increase in *T. ramosissima* germination in the laboratory. There were no significant effects on survival after germination or above- or belowground growth for either species, even at water salinities several times that of the Rio Grande. The presence of abundant seedlings of *P. fremontii* and *T. ramosissima* on sandbars along the Rio Grande in most years is consistent with our results.

Although salinity may play only a minor role in the colonization of newly deposited alluvial bars by *T. ramosissima* and *P. fremontii*, this factor can become more important over time. Over many years salt becomes concentrated on some floodplains as a result of evaporation and salt extrusion from *T. ramosissima* leaves. EC readings as high as 10.0 dS m^{-1} have been reported in floodplain sediment at the Bosque del Apache (John Taylor, Bosque del Apache National Wildlife Refuge, personal communication), and soil salinity levels as high as 60,000 mg l^{-1} occur on floodplain sites along the lower Colorado River (Jackson et al. 1990). Soil EC above 2.0 dS m^{-1} can reduce the growth of *P. fremontii* pole plantings (Anderson 1989). *T. ramosissima* has been shown to be less susceptible than *P. fremontii* to many of the negative effects of higher salinities (Brotherson and Winkle 1986, Jackson et al. 1990). *Tamarix* species avoid harmful effects of salts through extrusion from leaves and cellular compartmentation (Berry 1970, Kleinkopf and Wallace 1974, Waisel 1991).

Our results could be applied to efforts to revegetate riparian areas from seed. Riparian revegetation in the Southwest has largely consisted of planting poles or potted shoot cuttings. Although these approaches have been successful in some areas (Anderson et al. 1990), they can cost up to $10,000 per hectare (Ohmart et al. 1988). Furthermore, they require the destruction of parts of existing trees, and often entire trees or stands. Finally, these approaches may require importing cuttings or poles adapted to different site conditions. One alternative is regeneration of native cottonwoods and willows using natural seedfall (Friedman 1993, John Taylor personal communication). This approach generally involves clearing and irrigating an area so that seeds from nearby trees can colonize it. Our results suggest that water as saline as 37.4 meq l^{-1} (EC 3.45 dS m^{-1}) can be used to grow *P. fremontii* from seed on sand (Tables 1, 2). However, care must be taken to prevent long-term salt accumulation through evaporation (e.g., through periodic flooding to flush salts) and to avoid sites with preexisting high salinity. Use of water with low salinity can help prevent negative effects on *P. fremontii* and may decrease the germination rate of *T. ramosissima* (Table 3). However, in a restoration effort along the Cache la Poudre River, *T. ramosissima* became established in large numbers along with *P. deltoides* in spite of use of water of low salinity (Douglas Gladwin, National Biological Survey, personal communication). Therefore, low salinity will not prevent establishment of *T. ramosissima* from seed when moisture, a bare sediment, and a seed source are present.

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NAMES AND TYPES OF *HEDYSARUM* L. (FABACEAE) IN NORTH AMERICA

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ABSTRACT.—The names and types of *Hedysarum* L., sensu stricto, for North America are included, along with bibliographic citations, type information and place of deposit of types, and all synonyms. Lectotypes are designated for *Hedysarum auriculatum* Eastw., *H. carnulosum* Greene, *H. marginatum* Greene, *H. pabulare* A. Nels., and *H. truncatum* Eastw.

Key words: Hedysarum, *types, nomenclature.*

The following list of names and types in *Hedysarum* L. was prepared preliminary to submittal of a summary revision to the Flora North America Project. The genus *Hedysarum* L. as here interpreted for American taxa extends from the Bering Strait to Newfoundland and Vermont, and from the Polar Sea and the Canadian Arctic Archipelago south through the mountains and plains of western North America to Oklahoma, New Mexico, Arizona, and Nevada. Excluded from this treatment are those taxa originally included in *Hedysarum*, which are now interpreted as belonging to other genera, i.e., to *Desmodium*. The genus in the restricted sense consists of two complexes, i.e., those with leaflets thickened and veins obscured (the *boreale* complex) and those with relatively thin leaflets in which the veins are rather readily apparent (the *alpinum* complex). The earliest taxon within *Hedysarum alpinum* complex is that by Michaux (1803), who established the trinomial *Hedysarum alpinum americanum* Michx. The *boreale* complex was initiated by Nuttall (1818) with the publication of *H. boreale*.

Taxa in the two complexes demonstrate remarkable morphological and geographical parallelism. Each consists of additional taxa separable generally into two geographical subgroups juxtaposed at or near the 50th parallel of longitude (somewhat north of the Canada-U.S. boundary). North of that parallel lies most of *H. boreale* ssp. *mackenzii* (Richards.) Welsh, and most of *H. alpinum* sensu stricto. To the south occurs *H. occidentale* Greene, most of *H. sulphurescens* Rydb., limited extensions of *H. alpinum* L., and most of *H. boreale* ssp. *boreale*. Glacial events during the Pleistocene have been suggested as having separated the subsets, allowing them to achieve the degree of morphological and genetic integrity of the present populations. The present juxtaposition is suggested to have resulted by expansion of the respective entities into areas previously occupied by glaciers.

The rather large number of names involved in the genus is indicative of variation inherent in the various taxa. Flower size, plant size, leaflet size, and pubescence are features variable in both complexes. Apparent correlation of two or more of these features has served as justification for several names. Indeed, when one observes dwarf, large-flowered plants in either complex, there appears to be a compelling need for their recognition. However, much, if not all, of the variation is haphazard, or the attempt at segregation devolves to use of a single characteristic, such as presence or absence of pubescence, which fails also. There are few truly diagnostic characteristics once the two complexes are separated. The taxonomist ultimately must rely on a series of varying features to identify a particular specimen. Fortunately, the taxa are, with some notable exceptions, disjunct from each other. If the disjunction is not apparent from examination of a distribution map, it is often apparent in the field where the plants grow in different habitats. For example, the range of yellow-flowered *H. sulphurescens* apparently overlaps that of pink-purple–flowered *H. occidentale* in large part; yet, they seldom occur together, and only an exceptional intermediate is known.

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There are, in spite of gross similarities of the taxa within the respective complexes, few recorded intermediates.

Adding to the difficulties of interpretation of the North American materials is the interrupted circumboreal distribution of *H. alpinum*, a species with several close allies in Siberia. The initial interpretation by Michaux of North American *H. alpinum* as being taxonomically different ("*H. alpinum: americanum*") from that of the Old World has paraded apparition-like through most subsequent treatments of the genus. Unpublished work by Northstrom (1974) refuted the claim to difference between Siberian and American phases of the species, at least as far as broad categories were concerned. The claim that North American materials constitute a separate entity is likewise refuted by comparison of specimens from Siberia and North America in the present study. Other workers have asserted that large-flowered, low-growing plants of the species are identical with substantial Asian taxa [i.e., *H. hedysarioides* (L.) Schinz & Thellung (*Astragalus hedysarioides* L.)]. Such claims were investigated by Northstrom (1974), who determined that there is little basis for such assertions. Evidence to support the conspecific nature of the supposed entities is apparent when localities of such supposed taxa in western Alaska are examined and plants with larger flowers are found to occur within populations having small flowers, and that flower size within the species in a broad sense forms a continuum. And, occasional tall specimens within the *alpinum* complex also bear large flowers.

Another factor leading to the creation of a large number of synonyms was the early misinterpretation of specimens of *H. alpinum* under the name *H. boreale*. This switching of names, while not uniquely a problem in this genus, became of great importance to those workers who encountered the genus piecemeal and treated the variants as though they had not already been named. It was not helpful, perhaps, that the most ardent authors of western American plant names should be involved with the genus (i.e., Edward L. Greene, Per Axel Rydberg, and Aven Nelson). Greene, as the record indicates, was prone to name the same species several times in this and other genera, not recognizing, or possibly not caring, that he was renaming the same taxon.

Still another trend resulting in the formation of inconsequential names was the well-intentioned effort to provide epithets for specimens differing in insubstantial ways, i.e., the naming of white-flowered or teratological specimens as formae.

The following list is thought to be exhaustive for *Hedysarum* names in North America. Pertinent types have been received on loan through the kindness of curators of herbaria cited with the specimens. Abbreviations for herbaria are those standard ones cited in Index Herbariorum. Type information is presented below in dual format for some taxa, with type information (type locality) as recorded with the protologue cited first and label data of the type specimen (type) cited second where there is a substantial difference in the two accounts.

Hedysarum albiflorum **(Macoun) Fedtsch.**, Acta Hort. Petrop. 19: 252. 1902.
Basionym: *H. boreale* var. *albiflorum* Macoun
= *H. sulphurescens* Rydb.

Hedysarum alpinum **L.**, Sp. Pl. 750. 1753.
Type locality: "Habitat in Siberia" (Linnaeus l.c.).
Type: Possible lectotype 921.54 LINN (microfiche BRY!).

Hedysarum alpinum **var. *americanum*** **Michx.**, Fl. Bor. Amer. 2: 74. 1803.
= *H. alpinum* L.
Synonyms: *H. alpinum* ssp. *americanum* (Michx.) Fedtsch., Acta Hort. Petrop. 19: 255. 1902, in part; *H. americanum* (Michx.) Britt., Mem. Torrey Bot. Club 5: 201. 1894.
Type locality: "In borealibus Canadae, et in cataractis montium alleghanis."
Type: "Hedys. J ii p. 74–75. Herb. Mx" (isotype NY!).

There is a mounted half herbarium sheet at NY Torrey! bearing a large portion of a stem with a leaf and mature, strigose fruit of *H. boreale* var. *boreale*. This specimen is apparently superfluous (probably having been added later when additional material became available to Dr. Torrey from western American collections), but more pertinent to the present case the sheet also has an attached fragment envelope on which is written the type information noted above. The envelope contains a portion of an inflorescence, a flower, and several immature loment segments. The segments are glabrous, have a definite winged margin, and are identifiable as *H. alpinum* L. It is probable that the specimen from which the fragments were removed is with the Michaux herbarium at P.

Continued recognition of the American materials of *H. alpinum* at any infraspecific rank is fraught with difficulties; there are no diagnostic features known that will allow segregation of the American specimens from the Asiatic ones.

Hedysarum alpinum **var.** ***americanum*** **f.** ***albiflorum*** **(Standl.) Fern.,** Rhodora 35: 275. 1933.

Basionym: *H. americanum* f. *albiflorum* Standl.

= *H. alpinum* L.

The publication by Fernald (1933) recognizes white-flowered plants from Newfoundland.

Hedysarum alpinum **var.** ***grandiflorum*** **Rollins,** Rhodora 42: 233. 1940.

Type: "Newfoundland, Pistolet Bay, Mossy and turfy trap cliffs and talus, Anse aux Sauvages, M. L. Fernald, K. M. Wiegand and Bayard Long 28625, August 11, 1925"; holotype GH!

Paratype: "New Foundland, Region of Port a Port Bay, No. 10849. In humus or turf on the limestone tableland, altitude 200–300 m., Table Mountain, M. L. Fernald and H. St. John, July 16 & 17, 1914" (CAN!; BM!).

This name is based on large-flowered (about 16 mm long), low-growing specimens from Newfoundland. There are other similar plants scattered through much of the distribution of *H. alpinum* in North America, but they are more consistently represented in frigid or other inhospitable arctic or subarctic sites. Even in the type series cited with the protologue there is considerable variation. The paratype cited above differs significantly from the holotype specimen; it is much taller and has flowers of a size intermediate with those of specimens more usual for var. *alpinum* in a more strict sense. Indeed, the low-growing, larger-flowered phase appears to be a phenotypically recurring recombinant form within a complex exhibiting much variation in flower size and other features. However, size of flower is not always correlated with plant height or flower number. All possible combinations of flower size, flower number, and plant height are represented in the species as a whole. It is possible to write a key that will separate these plants, but it seems that such a key will not then be segregating natural taxa.

Hedysarum alpinum **ssp.** ***philosocia*** **(A. Nels.) Love & Love,** Taxon 31: 347. 1982.

Basionym: *H. philosocia* A. Nels.

= *H. alpinum* L.

Hedysarum alpinum **var.** ***philosocia*** **(A. Nels.) Rollins,** Rhodora 42: 224. 1940.

Basionym: *H. philosocia* A. Nels.

= *H. alpinum* L.

Hedysarum americanum **(Michx.) Britt.,** Mem. Torrey Bot. Club 5: 202. 1894.

Basionym: *H. alpinum* var. *americanum* Michx.

= *H. alpinum* L.

Hedysarum americanum **f.** ***albiflorum*** **Standl.,** Field Mus. Pub. Bot. 8: 15. 1930.

= *H. alpinum* L.

Synonym: *H. albiflorum* (Macoun) Fedtsch.

Type: "Alaska: Davidson Glacier, July 4, 1929, William S. Cooper & Frances E. Andrews 95 (Herb. Field Mus. No. 598,264, type)"; holotype F!

White-flowered specimens occur sporadically through populations of taxa with generally pink-purple flowers. Their recognition at any taxonomic rank is probably moot, and the publication of the taxon by Standley (1930) is therefore inconsequential.

Hedysarum americanum **var.** ***mackenzii*** **(Richards.) Britt.,** Mem. Torrey Bot. Club 5: 202. 1894.

Basionym: *H. mackenzii* Richards.

= *H. boreale* ssp. *mackenzii* (Richards.) Welsh

Hedysarum auriculatum **Eastw.,** Bot. Gaz. 33: 205. 1902.

= *H. alpinum* L.

Type: Alaska, Cape Nome, Blaisdell s.n. summer 1900 (lectotype selected here: GH!, isolectotype US!).

Specimens on which *H. auriculatum* is based were distributed from the California Academy of Sciences herbarium with collection information recorded on labels of that institution. The only known specimens in contemporary collections are those at GH and US. The two specimens consist of almost identical branches of *H. alpinum*, with both flowers and fruit, although that at GH is designated on the label as a duplicate of the type, which was presumably at CAS prior to the San Francisco earthquake early in this century. Fire resulting from that devastating tragedy destroyed much of the early Academy herbarium.

Hedysarum bakeri **Greene ex Rydb.,** Bull. Agric. Exper. Sta. Colorado, 100: 215. 1906. pro syn.

= *H. boreale* Nutt. var. *boreale*

Intended type: "Flora of Colorado. Plants the Gunnison Watershed, Cimarron, June 28. Stems in large clusters 8 in. to 1 1/2 ft. on dry open slopes. Collected in 1901 by C. F. Baker, No. 274" (NDG!).

Evidently the name was never published by E. L. Greene but was cited as a synonym of *H. pabulare* A. Nelson by Rydberg in his Flora of Colorado. The intended type has three mounted stems showing flowers and maturing fruit; they are strigose both on herbage and on the loments. The plants differ in no material way from a great many specimens from Colorado. Perhaps Greene also realized as much.

Hedysarum boreale **Nutt.,** Gen. N. Amer. Pl. 2: 110. 1818.

Type locality: North Dakota, "around Fort Mandan, on the banks of the Missouri," Nuttall (l.c.).

Type: "Hedysarum boreale—Sources of the Missouri," Nuttall (probably late June) 1811; holotype BM!

The name *H. boreale* was early transferred to the concept of *H. alpinum*, and part of the synonymy reflects attempts by various authors to resolve the apparent lack of a name for this wide-ranging and highly variable species. Nuttall (Torrey and Gray 1838) named the species a second time, as *H. canescens*, based on specimens from along the Snake River in present Idaho taken in 1834. He was in the vicinity of Fort Hall, Idaho, from 14 July to 6 August 1834 (McKelvey 1955: 602). Whether he noted the similarity between earlier- and later-named materials is not known. It seems likely that he did not have authentic material of the earlier-named taxon at hand for comparison with his collections on the 1834 Wyeth expedition. The type at BM, a solitary flowering stem, is mounted with several flowering stems of *H. alpinum* of unknown collector.

Hedysarum boreale **var. *albiflorum*** **Macoun**, Cat. Canad. Pl. 1: 510. 1884. nom. nud.
= *H. sulphurescens* Rydb.
Syn: *H. albiflorum* (Macoun) Fedtsch.
Type locality: "This form is peculiar to the foothills and drier mountain slopes, and is abundant from the Kananaskis through the Rocky Mountains to the Columbia valley at Donald, Lat. 51° (Macoun). Eastern summit of the North Kootanie Pass, Rocky Mountains" (l.c.).
Type: "Geological and Natural History of Canada. No. 1111.5390. Hedysarum boreale var. albiflorum. Dry soil. East summit of North Kootanie Pass, R. Mts. Dawson. July 29th 1883" and "Geological and Natural History Survey of Canada. No. 533, 5389. Hedysarum boreale Nutt. var. alba. Macoun. Mountain slopes. Kananaskis. Rocky Mts. Macoun. June 24th 1885"; syntypes CAN!

There is no description aside from the designation "albiflorum" proposed as an epithet. The only other information provided by Macoun aside from that related with the locality data is the statement: "This fine plant is closely related to *H. boreale*, but is certainly distinct." The name is regarded as a nomen nudum. The collection by Dawson is, nevertheless, an excellent flowering example of *H. sulphurescens*, and the Macoun sheet consists of two plants with both flowers and immature to mature fruits, both also *H. sulphurescens*. The indication by Macoun of relationship of var. *albiforum* to *H. boreale* reflects the general misapplication by many American botanists of *H. boreale* to the *alpinum* complex in North America, of which *H. sulphurescens* is a portion. Macoun used the number 533 for several collections of *Hedysarum* taken from 1883 to 1885.

Hedysarum boreale **var. *cinerascens*** **(Rydb.) Rollins**, Rhodora 42: 234. 1940.
Basionym: *H. cinerascens* Rydb. et *H. canescens* Nutt. in seq.
= *H. boreale* Nutt. var. *boreale*

Hedysarum boreale **var. *cinerascens*** **f. *album*** **Boivin**, Naturaliste Canad. 87: 34. 1960.
= *H. boreale* Nutt. var. *boreale*
Type: "Canada, Saskatchewan, Maple Creek District, Eastend, hillside along river valley, 19 July 1950, R. C. Russell S 5075" (holotype at DAO!).

Hedysarum boreale **var. *flavescens*** **(Coult. & Fisher) Fedtsch.**, Bull. Herb. Boiss. 7: 256. 1899.
Basionym: *H. flavescens* Coult. & Fisher
= *H. sulphurescens* Rydb.

Hedysarum boreale **var. *gremiale*** **(Rollins) Northstrom & Welsh**, Great Basin Nat. 30: 125. 1970.
Basionym: *H. gremiale* Rollins

Hedysarum boreale **var. *leucanthum*** **(Greene) M. E. Jones**, Proc. Calif. Acad. Sci. 5: 677. 1895.
Basionym: *H. mackenzii* var. *leucanthum* Greene
= *H. boreale* ssp. *mackenzii* (Richards.) Welsh

Hedysarum boreale **ssp. *mackenzii*** **(Richards.) Welsh**, Great Basin Nat. 28: 152. 1968.
Basionym: *H. mackenzii* Richards.

Hedysarum boreale **var. *mackenzii*** **(Richards.) C. L. Hitchc.**, Vasc. Pl. Pacific N. W. 3: 275. 1961.
Basionym: *H. mackenzii* Richards.

Hedysarum boreale **var. *mackenzii*** **f. *niveum*** **(Boivin) Boivin**, Naturaliste Canad. 93: 433. 1966.
Basionym: *H. mackenzii* var. *mackenzii* f. *niveum* Boivin
= *H. boreale* ssp. *mackenzii* (Richards.) Welsh

Hedysarum boreale **var. *obovatum*** **Rollins**, Rhodora 42: 235. 1940.
= *H. boreale* Nutt. var. *boreale*
Type: Nevada, Elko County, Thorpe Creek, E of Lamoile, 25 July 1928, H. H. Price 168 (holotype photo RM!).

Hedysarum boreale **f. *proliferum*** **(Dore) Boivin**, Naturaliste Canad. 94: 630. 1967.
Basionym: *H. mackenzii* f. *proliferum* Dore
= *H. boreale* ssp. *mackenzii* (Richards.) Welsh

Hedysarum boreale **var. *utahense*** **(Rydb.) Rollins**, Rhodora 42: 235. 1940.
Basionym: *H. utahense* Rydb.
= *Hedysarum boreale* Nutt. var. *boreale*

Hedysarum canescens **Nutt.**, in Torr. & Gray, Fl. N. Amer. 1: 357. 1838. Not *H. canescens* L.
Basionym: *H. cinerascens* Rydb.; *H. boreale* var. *cinerascens* (Rydb.) Rollins
= *H. boreale* Nutt. var. *boreale*
Type locality: Idaho, "Plains of the Rocky Mountains, particularly near Lewis's River," Nuttall (l.c.)
Type: "Hedysarum * canescens. H. mackenzii? Hook. R. Mts. Lewis [Snake] R." Nuttall s.n. (probably in July) 1834 (holotype PH!; isotypes GH!, BM!, 2 sheets?).

The specimen at PH (which is mounted on a sheet with two other superfluous collections) bears the date "July 12," with the incorrect year date 1833 obviously added later. Nuttall was with the Wyeth Expedition in 1834, and on 12 July was a short distance east of where Fort Hall would be constructed subsequently. Despite the existence of the earlier-named *H. boreale*, with which *H. canescens* is synonymous, this name or its substitutes would be featured prominently in 19th-century accounts of the genus in the American West. There are two of Nuttall's specimens on the sheet at GH, each provided with a label—both with flowers and both representing the same taxon. The label information consists of the following: "Hedysarum * canescens. H. mackenzii? R. Mts.," and Hedysarum * canescens R. Mts." Since no additional locality information or date accompanies the labels, the status as exact duplicates is unknown. It seems likely that both were included within the concept of *H. canescens* by Nuttall, and both can be regarded as isotypes. There is a second possible isotype of *H. canescens* at BM, "Hedysarum mackenzii? Fort Hall. Prairie, common. Aug." It lacks the * usual for Nuttall's labels, and his name is not in evidence, but the handwriting appears to be his.

Hedysarum carnulosum **Greene,** Pittonia 3: 212. 1897.
= *H. boreale* Nutt. var. *boreale*
Type locality: "Common in clayey soil about the mouth of the Canon of the Arkansas, in southern Colorado" (Greene l.c.).
Type: Colorado, Fremont Co., "Plants of Colorado, Canon City, 8 Sept. 1896, Edw. L. Greene" (lectotype here designated: NDG!, 2 isolectotypes also NDG!).

While no specimens were cited with the original description, the three specimens so named in Greene's handwriting at NDG are most certainly type material. All bear the same date and locality information. The specimen bearing the "Greeneanum Herbarium" number 35686 is here chosen as lectotype; the others, 35687 and 35688, are considered isolectotypes. The lectotype has both flowers and fruit; the other two are in fruit and flower (with immature fruit), respectively. All have strigose herbage and loments. Usual flowering time for the species is April to late July. Is it possible that the species flowered again following late summer rains at Canon City in September 1896?

Hedysarum cinerascens **Rydb.,** Mem. N. Y. Bot. Gard. 1: 257. 1900. nom. nov. pro *H. canescens* Nutt.
= *H. boreale* Nutt. var. *boreale*
Basionym: *H. canescens* Nutt.
Syn: *H. boreale* var. *cinerascens* (Rydb.) Rollins

This material was retained by Northstrom (1974) at varietal rank. The taxon stands on the sole character of pubescence, and a plotting of the distribution of hairy versus glabrous plants demonstrates much overlap. The specimens can be separated, but do they represent taxa?

Hedysarum flavescens **Coult. & Fisher,** Bot. Gaz. 18: 300. 1893, non Regel & Schmalh.
Basionym of: *H. sulphurescens* Rydb.
Type: Montana, near Helena, May 1892, F. D. Kelsey s.n. (holotype F!).

It is unfortunate that the epithet *flavescens* was occupied; it fits well the description of flower color in this taxon. Many of the Kelsey collections are in the U.S. National Museum (Elisens 1985), but the type of *H. flavescens* is at F, where Coulter's herbarium is deposited.

Hedysarum gremiale **Rollins,** Rhodora 42: 230. 1940.
= *H. boreale* var. *gremiale* (Rollins) Northstrom & Welsh
Type: Utah, Uintah County, "ca 14 mi W. of Vernal, 16 June 1937," R. C. Rollins 1733 (holotype GH!, isotypes RM!, US!, CAS!, UTC!, MONTU!, PH!, F!).

This taxon stands on the feature of lateral spines on the loment segments; it is otherwise indistinguishable from plants of var. *boreale* by which it is surrounded (Northstrom and Welsh 1970).

Hedysarum lancifolium **Rydb.,** Mem. New York Bot. Gard. 1: 256. 1900.
= *H. occidentale* Greene
Type: "Mountain woods near head waters of Jocko River, Montana,—flowers pale purple, W. M. Canby 93, July 15, 1883" (holotype NY!).

The type specimen consists of a folded plant some 75 cm tall bearing leaves and flowers, and a stem fragment bearing immature fruit. Mature flowers are about 16 mm long, on the short side of the variation in *H. occidentale*, but the fruit, even though immature, is of the size and form of that species.

Hedysarum leucanthum **(Greene) Greene,** Pittonia 3: 213. 1897.
Basionym: *H. mackenzii* var. *leucanthum* Greene
= *H. boreale* ssp. *mackenzii* (Richards.) Welsh

Hedysarum mackenzii **Richards.,** in Franklin, 1st Journey Bot. Append. 745. 1823.
= *H. boreale* ssp. *mackenzii* (Richardson) Welsh
Type: Canada, Barren grounds, Point Lake to the Arctic Sea, Richardson s. n. [holotype BM (photo CAN!), isotype NY Columbia! "Hedysarum mackenzii. Franklin's Journey. Dr. Hooker," isotype PH!; "Astr. (crossed out) Hedys. Mackenzii Richard. N. W. Amer. Fr. Exp. Dr. Ho." and "Herb. A. Gray. H. Mackenzii. Torr. & Gray, Fl. N. Amer. Richardson (B.D.G.)," isotypes GH!].

Evidently Dr. William Jackson Hooker sent representative material obtained by John Richardson, botanist with the Franklin expedition, to the Philadelphia Academy and to John Torrey and Asa Gray. Collections from the Franklin expedition demonstrate the variability represented in a rather large set of specimens, each matched by modern collections of the taxon. The second sheet cited at GH is doubly mounted with a mere fragment presumed to have come from the Franklin expedition in the lower portion and a second fragmentary collection by Burke (apparently a phase of *H. boreale*) from the Rocky Mountains. The latter material is not a portion of the type of *H. mackenzii*.

Hedysarum mackenzii **var. *fraseri*** **Boivin,** Canad. Field-Nat. 65: 20. 1951.
= *H. boreale* Nutt. var. *boreale*
Type locality: Canada: "Saskatchewan: W. P. Fraser, Langham, river valley, June 12 and 26, 1938" (l.c.)
Type: "Hedysarum Mackenzii Richards. River valley, Langham, Sask., W.P.F[raser]., June 12 & 26, 1938" (holotype DAO!).

Boivin (l.c.) cites the revisionary treatment of Rollins (1940) as indicating that *H. mackenzii* var. *mackenzii* has flowers 18–21 mm long, but with some 16–20 mm. Prairie plants from Saskatchewan and Alberta, however, have flowers 13–15 mm long. These latter plants are the basis of his var. *fraseri*. The type of var. *fraseri* represents *H. boreale* ssp. *boreale* var. *boreale*, which is present along the plains and foot slope of the Rocky Mountains, and has flowers of the size indicated for the variety.

***Hedysarum mackenzii* var. *leucanthum* Greene**, Pittonia 2: 294. 1892.

Basionym of: *H. leucanthum* (Greene) Greene
= *H. boreale* ssp. *mackenzii* (Richards.) Welsh
Type locality: "On the Porcupine River, northern Alaska, Mr. J. J. Turner" (Greene l.c.).
Type: "Plants of Alaska, collected on the Porcupine River, 1891, Mr. J. Turner" (holotype NDG!).

Greene (1892) notes that this is "far more than an albino state of *H. Mackenzii*; perhaps identical with some asiatic species; but the plants were just coming into flower when gathered, in that there is no trace of the loment." He later (1897) elevated it to species rank. However, except for white flowers, which occur with some frequency in the species, the plant differs in no respect from numerous other plants from the arctic range of the taxon generally.

***Hedysarum mackenzii* var. *mackenzii* f. *niveum* Boivin**, Canad. Field-Nat. 65: 20. 1951.

Basionym of: *H. boreale* var. *mackenzii* f. *niveum* (Boivin) Boivin
= *H. boreale* ssp. *mackenzii* (Richards.) Welsh
Type: "Yukon Territory: J. W. Abbott 17a, Pine Creek, sandy land, June 7, 1946" (holotype DAO!).

The collection consists of five flowering stems of *H. boreale* ssp. *mackenzii*, all with white flowers. The condition of white flowers is occasional throughout the subspecies and hardly worthy of taxonomic consideration.

***Hedysarum mackenzii* var. *pabulare* (A. Nels.) Kearney & Peebles**, J. Wash. Acad. Sci. 29: 485. 1939.

Basionym: *H. pabulare* A. Nels.
= *Hedysarum boreale* Nutt. var. *boreale*

***Hedysarum boreale* var. *leucanthum* (Greene) M. E. Jones**, Proc. Calif. Acad. II. 5: 677.

= *H. boreale* ssp. *mackenzii* (Richards.) Welsh
Syn: *H. leucanthum* (Greene) Greene

***Hedysarum mackenzii* f. *proliferum* Dore**, Canad. Field-Nat. 73: 151. 1959.

Basionym of: *H. boreale* f. *proliferum* (Dore) Boivin
= *H. boreale* ssp. *mackenzii* (Richards.) Welsh
Type: "Plants of Alaska. A single clump in shallow soil over broken rock (growing beside common petaliferous plant, cf. 4983). North Side of Tanana River, Mile 277, Richardson Highway, 64°10′N, 145°52′W, W. J. Cody & T. J. M. Webster 4984, June 3, 1951" (holotype DAO!).

This name is based (Dore 1959) on a teratological specimen of *H. boreale* ssp. *mackenzii*, a recurring variant induced by a pathogen, likely a smut-fungus. Teratology occurs in several if not all boreal legumes native to Alaska. In certain of those instances the inflorescence typically elongates, flowers become erect on attenuated pedicels, petals are deformed, and the ovary is typically exserted from the flower. In some specimens at least the ovary is filled with black spores. The type specimen of f. *proliferum* exhibits another variant than that typically encountered. The inflorescence is shortened and modified flower buds are in tight clusters. Whether elongate or compact, specimens on which such aberrations are based are not taxa, and the need to name them is therefore moot.

***Hedysarum macquenzii* f. *canescens* (Nutt.) Fedtsch.**, Acta Hort. Petrop. 19: 272. 1902.

Basionym: *H. canescens* Nutt.
= *H. boreale* Nutt. var. *boreale*

***Hedysarum marginatum* Greene**, Pittonia, 4: 138. 1900.

= *H. occidentale* Greene
Type locality: "Mountains above Cimarron, southern Colorado, collected by the writer, 30 Aug. 1896; also near Pagosa Springs, Colo., 26 July, 1899, C. F. Baker" (Greene l.c.).
Type: Colorado, "Plants of Colorado, Near Cimarron, 30 Aug. 1896, Edw. L. Greene" (lectotype NDG!, here chosen); "Plants of Southern Colorado, Pagosa Springs, 26 July 1899, C. F. Baker" (syntypes NDG!, NY!, RM!, GH!, F!).

The lectotype collected by Greene is in fruit; syntypes at NDG and NY have both flowering and fruiting branches. In both the loment articles are markedly winged and strigose; herbage is strigose also (see Greene 1900).

***Hedysarum occidentale* Greene**, Pittonia 3: 19. 1896.

Type locality: "Olympic Mountains, Washington, 1890, C. V. Piper" (Greene l.c.).
Type: Washington, "Olympic Mts., C. V. Piper 905, flowers 11 August 1890, fruit 30 Sept. 1890" (holotype NDG!).

Greene (1896) provides a description and a short note: "Plant like *H. boreale* when in flower, though with broader leaflets and widely different fruit." A second sheet from the Olympic Mountains at NDG!, Piper 2227 (August 1895), has the epithet "occidentale" in Greene's hand, but it was not cited by him. It is much better material than the type. For a long time the name *H. boreale* was included within the concept of *H. alpinum*. It is likely that Greene was under a similar misconception. The general aspect of *H. occidentale* (i.e., conspicuously veined leaflets and large loments with prominently reticulate venation), which occurs from Vancouver Island, British Columbia, and the Olympic Peninsula, Washington, disjunctly eastward to northern and eastern Idaho, western Montana, western Wyoming, northeastern Utah, and montane southern Colorado, is that of *H. alpinum*; and it differs generally in the manner indicated by Greene.

The most distinctive feature separating most, if not all, specimens of *H. occidentale* from *H.*

alpinum is the much larger, rather conspicuously wing-margined loment segments. Flowers are generally larger, often much larger. However, plants from the Absaroka Range of northwestern Wyoming approach *H. alpinum* in occasionally having small flowers, but when collected at maturity, the fruit is that of *H. occidentale*. Additional collections might demonstrate that *H. alpinum* per se is indeed in the Absarokas. Large-flowered plants of *H. alpinum*, mainly of frigid sites in the arctic, approach the size of flowers of some *H. occidentale* specimens, but the fruit there is that of *H. alpinum*. *H. occidentale* has loments very similar to those of the closely allied *H. sulphurescens*.

***Hedysarum occidentale* Greene var. *canone* Welsh**, Great Basin Nat. 38: 314. 1978.

Type: Utah, Carbon County, "ca 14 mi due ENE of Helper, Soldier Creek, 30 June 1977, Welsh & Taylor 15256" (holotype BRY!; isotype at NY!).

The syndrome of characters associated with this taxon is shared individually elsewhere within the species as a whole. However, specimens from Duchesne, Carbon, and Emery counties, Utah, and Gunnison County, Colorado, are recognizable by their large, thick, ovate to ovate-lanceolate, yellow-green leaflets, and large pale flowers. Plants are known from rather xeric sites in pinyon-juniper and mountain brush communities, whereas plants of the type variety are mainly of more mesic sites. Although the taxon is segregated on weak diagnostic features, it seems to be at least a trend worthy of taxonomic recognition. It has long been known in collections.

***Hedysarum pabulare* A. Nels.**, Proc. Biol. Soc. Wash. 15: 185. 1902.

= *H. boreale* Nutt. var. *boreale*

Type: Wyoming, Wind River, Dubois, A. Nelson 752, 1894 (lectotype here designated RM!).

This name is based on several Wyoming, Colorado, and Utah syntypes: i.e., M. E. Jones 5592, Soldier Summit, Utah, in 1894, POM?, BM!, F!; Snake River, Wyoming, A. Nelson 3496, 19 August 1899 RM!; Wyoming, Natrona Co., Bates Creek, L. N. Goodding 201, 5 July 1901, RM!, F!

***Hedysarum pabulare* var. *rivulare* L. O. Williams**, Ann. Missouri Bot. Gard. 21: 344. 1934.

= *H. boreale* Nutt. var. *boreale*

Type: Wyoming, Teton County, along the Snake River, 31 July 1932, L. O. Williams 975 (holotype RM!; isotypes GH!, CAS!).

***Hedysarum philoscia* A. Nels.**, Proc. Biol. Soc. Wash. 15: 185. 1902.

Basionym: *H. alpinum* var. *philoscia* (A. Nels.) Rollins; *H. alpinum* ssp. *philoscia* (A. Nels.) Love & Love

= *H. alpinum* L.

Type: Wyoming, Albany County, Head of Crow Creek, Laramie Mountains, 1896, A. Nelson 2034; holotype RM!

Material from the Black Hills of South Dakota and from southeastern Wyoming is morphologically similar and has been recognized as belonging to a taxon that survived south of the major glacial events of the Pleistocene. The main diagnostic criterion is, however, loment pubescence. That feature is inconstant within the southern material and often is present in plants far beyond its supposed range (which has been plotted to include plants as far north as the 50th parallel). Recognition of plants at any taxonomic rank is, therefore, problematical.

***Hedysarum roezlianum* Prantl**, Ind. Sem. Hort. Wirceb. 8. 1873.

= *H. boreale* Nutt. var. *boreale*?

I have been unable to find any reference to this taxon aside from its citation by Rollins (1940).

***Hedysarum sulphurescens* Rydb.**, Bull. Torrey Bot. Club. 24: 251. 1897.

Basionym: *H. flavescens* Coult. & Fisher, not Regel & Schmalh.

Yellow to yellowish flowers easily distinguish this entity, which shares the peculiar loment features of *H. occidentale*. The species ranges from the southern British Columbia–Alberta Rockies south through north central Washington, northern Idaho, western Montana, and northwestern Wyoming.

***Hedysarum truncatum* Eastw.**, Bot. Gaz. 33: 205. 1902.

= *H. alpinum* L.

Type: Alaska, Nome, Dr. F. E. Blaisdell s.n. summer 1900 (lectotype NY! here designated; isolectotype GH!).

Type material is low, about 2–2.5 dm tall, has mature flowers about 12 mm long, and has fruit the size and conformation of *H. alpinum*. It is identical for all practical purposes with material named by Eastwood simultaneously as *H. auriculatum* and taken at the same place and time by the same collector in 1900.

***Hedysarum uintahense* A. Nels.**, Proc. Biol. Soc. Wash. 15: 186. 1902.

= *H. occidentale* Greene

Type: Wyoming, "In draws of the foothills, Evanston, A. Nelson 7198, 14 June 1900" (holotype RM!; isotypes RM!, NY!, GH!).

Type sheets uniformly bear thick, lanceolate to lance-ovate leaflets similar to var. *canone*, but with flowers of typical *H. occidentale*. Plants from southwest Wyoming are not uniformly of the *uintahense* type, but vary from one population to another, with most being similar to traditional *H. occidentale*.

***Hedysarum utahense* Rydb.**, Bull. Torrey Bot. Club 34: 424. 1907.

= *H. boreale* Nutt. var. *boreale*

Type: Utah, Salt Lake County, "vicinity of Salt Lake City, Utah," Leonard 55, 26 May 1883 (holotype NY!).

The type consists of two complete stems and a fragmentary branch; it is typical of the material growing through much of Utah and elsewhere in the West.

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WHIPWORM (*TRICHURIS DIPODOMYS*) INFECTION IN KANGAROO RATS (*DIPODOMYS* SPP.): EFFECTS ON DIGESTIVE EFFICIENCY

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ABSTRACT.—To determine whether infections by whipworms (*Trichuris dipodomys* [Nematoda: Trichurata: Trichuridae]) might affect digestive efficiency and therefore energy budgets of two species of kangaroo rats (*Dipodomys microps* and *Dipodomys ordii* [Rodentia: Heteromyidae]), we compared the apparent dry matter digestibility of three groups of hosts: those naturally infected with whipworms, those naturally uninfected with whipworms, and those originally naturally infected but later deinfected by treatment with the anthelminthic Ivermectin. Prevalence of *T. dipodomys* was higher in *D. microps* (53%) than in *D. ordii* (14%). Apparent dry matter digestibility was reduced by whipworm infection in *D. microps* but not in *D. ordii*. Although a statistically significant effect was shown, its small magnitude indicates that whipworm infection is unlikely to have a biologically significant impact on the energy budgets of host kangaroo rats.

Key words: parasite, digestive efficiency, whipworm, kangaroo rat, Trichuris, Dipodomys, *energy budget.*

Parasites inhabiting the gastrointestinal tract of a host may reduce the efficiency of the organs they inhabit either through direct competition for nutrients or through damage to absorptive surfaces. Because decreased digestive efficiency may reduce the rate of energy input into a host, gastrointestinal parasites have the potential to cause a change in host energy allocation (e.g., reduced activity or reduced reproduction), and thereby impact the ecology of the host (Munger and Karasov 1989).

Tapeworm infections have a measurable effect on digestive efficiency, but a biologically unimportant effect on the energy budget of host white-footed mice (*Peromyscus leucopus;* Munger and Karasov 1989). The present study was designed to determine if infection by a nematode, the whipworm *Trichuris dipodomys*, has a substantial effect on one aspect of the energy budget, digestive efficiency, of host kangaroo rats (*Dipodomys microps* and *D. ordii*).

MATERIALS AND METHODS

Our study site, located 2 km N of Murphy, Owyhee County, ID, is in desertscrub habitat with sandy loam substrate. Primary shrub species of the study area are *Artemisia spinescens, Artemisia tridentata, Atriplex canescens, Atriplex confertifolia, Atriplex spinosa*, and *Chrysothamnus nauseosus.* Six rodent species were captured at the site, *Ammospermophilus leucurus, Neotoma lepida, Perognathus flavus, Peromyscus maniculatus*, and two species of kangaroo rats, *Dipodomys ordii* and *Dipodomys microps. Dipodomys ordii* ranges from 42 to 72 g and consumes a diet consisting primarily of seeds (Zeveloff 1988). *Dipodomys microps* is larger, 72–91 g, and is unique among kangaroo rats in that it relies heavily on leaves of *Atriplex confertifolia* for forage (Kenagy 1972, Zeveloff 1988). Both species are liable to infection by the whipworm *Trichuris dipodomys*, a nematode that inhabits the cecum of infected hosts (Grundmann 1957, Whitaker et al. 1993).

On the study site we established a 13 × 13 grid of 169 Sherman live traps baited with millet and placed at 15 m intervals. During two trapping sessions, 14–22 June and 15–18 August 1990, kangaroo rats (30 individuals of *D. microps* and 85 of *D. ordii*) were captured and brought into the laboratory. Fecal specimens from each animal were analyzed for the presence of parasite eggs by standard centrifugal flotation techniques using saturated sucrose solution (Pritchard and Kruse 1982). Six infected but untreated animals from the June experiment were included in the pool of animals used in the August experiment. The few animals that failed to thrive in the lab were removed from the experiment; data from a

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total of 29 *D. microps* individuals and 56 *D. ordii* were analyzed.

Each month's set of captures was subjected to the following protocol:

(1) Kangaroo rats were acclimated to a diet of millet seed for 3–11 d.

(2) A pretreatment feeding trial was performed: Animals were placed in wire-bottomed cages with a measured amount of whole millet seed. At the end of 5 d, fecal pellets were separated from spilled food and dried >24 h at 50° C. Initial digestive efficiency of each animal was measured as apparent dry matter digestibility (i.e., the proportion of mass consumed but not lost as waste), which was calculated as $(M_{FO} - M_{FE}) / M_{FO}$, where M_{FO} and M_{FE} are the mass of food consumed and feces produced, respectively.

(3) Half of the infected animals were then injected subcutaneously with a solution of Ivermectin (a systemic anthelminthic; Ivomec brand, from MSD AGVET, Rahway, NJ). Figure 1 gives sample sizes of treatment groups. June captures received, on each of two consecutive days, a 0.2-cc injection of Ivermectin in 40% glycerol formal and 60% propylene glycol; each injection delivered ca 350 μg Ivermectin / kg body mass. Controls received equal-volume injections of the glycerol formal–propylene glycol carrier. This dosage had little effect on the presence of whipworm eggs in feces of injected animals. Therefore animals received 8 d later a second set of two injections, each of 0.15 cc and delivering ca 2 mg Ivermectin / kg body mass; control animals received the carrier. August captures received, on each of two consecutive days, an injection of 0.15 cc volume delivering ca 2 mg Ivermectin / kg body mass. Control animals received the carrier. To control for possible side effects of Ivermectin, half of the uninfected animals captured in August were also injected with a solution of Ivermectin.

(4) Two days after each set of injections a posttreatment feeding trial was conducted using techniques in (2) above. Only results of the pretreatment feeding trials and feeding trials following the 2-mg Ivermectin / kg body mass injection will be presented below.

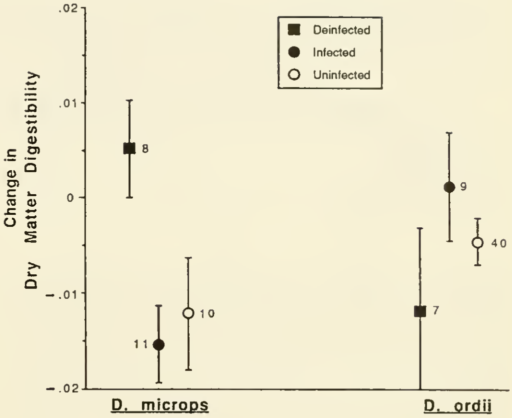

Fig. 1. Effects of variation in parasite load on proportional change in dry matter digestibility. Means ± SE. Numbers represent sample sizes.

RESULTS AND DISCUSSION

Adult worms (seven of each gender) taken from a *Dipodomys microps* at our site were identified as *Trichuris dipodomys*. Although some minor morphological differences from the original species description (Read 1956) do exist, perhaps as a result of geographical variation, the specimens most closely match Read's description of *T. dipodomys* (A. Shostak personal communication). Measurements of several key morphological characters are as follows ($\bar{X}$ ± SD): total length: ♂ 25.6 ± 0.8 mm, ♀ 41.3 ± 2.9 mm; hindbody length: ♂ 12.7 ± 0.4 mm, ♀ 23.7 ± 1.9 mm; spicule length: 850 ± 85.1 μm; egg length: 64.8 ± 5.0 μm; egg width: 33.5 ± 1.0 μm. Voucher specimens were deposited with the University of Alberta Parasite Collection (#'s UAPC11464 and UAPC11465). Although we did not identify whipworms from *D. ordii*, we are confident they are *T. dipodomys*; the type host for *T. dipodomys* is *D. ordii*, and *T. dipodomys* is known only from *D. ordii* and *D. microps* (Whitaker et al. 1993).

Prevalence in Host Species.

Trichuris dipodomys occurred at substantially higher prevalence in *D. microps* than in *D. ordii* (Table 1), a result similar to that of Grundmann (1957). We can speculate as to three possible explanations for this pattern. The first is that eggs produced by adult worms in *D. microps* may become embryonated more easily than those in *D. ordii*. Freshly produced fecal pellets of *D. microps* appear moister than those of *D. ordii* (Munger personal observation), probably because of the higher amount of green or leafy vegetation in the diet of *D. microps*. If moisture is necessary for embryonation of the eggs (as is implied by Parry 1968),

TABLE 1. Infection of two species of kangaroo rat with the nematode *Trichuris dipodomys*.

	D. microps		*D. ordii*	
	Infected	Uninfected	Infected	Uninfected
June trapping	10	5	5	39
August trapping	6	9	7	34

moister feces may lead to higher embryonation rates and therefore higher prevalence among *D. microps*. The second explanation is that social and burrow use behavior may differ between these species. For example, perhaps *D. microps* individuals visit one another's burrows (and thereby become exposed to parasite eggs) at a substantially higher frequency than do *D. ordii*. Also, *D. microps* inhabits a mound up to 2 m in diameter while *D. ordii* inhabits less substantial individual holes. Studies of another system of two species of kangaroo rats has shown that the larger, mound-inhabiting *D. spectabilis* uses its burrow system for prolonged periods, while the smaller *D. merriami* rotates among several burrows (Jones 1989). This latter behavior would tend to reduce reinfection of individuals; it would be interesting to see if behaviors differ similarly between *D. microps* and *D. ordii*. The third explanation is that resistance to infection may differ between these two host species.

Effects on Digestive Efficiency

Apparent dry matter digestibility (ADMD) of millet seed was quite high, >95% on average (Table 2), a figure comparable to that found by Schrieber (1979) for granivorous rodents. Injection of Ivermectin did not appear to affect ADMD of animals uninfected by whipworms, an effect that might occur through the removal of other symbionts, or through some direct effect (proportional change in ADMD, $\bar{X}$ ± SE; untreated: –0.0043 ± 0.0035, treated: –0.0058 ± 0.0037). Therefore, in the following analyses all naturally uninfected animals are combined into one class.

The effect of whipworm removal on ADMD was analyzed with a two-way analysis of variance (ANOVA). One factor analyzed was the treatment: deinfected (naturally infected but treated with Ivermectin) vs. infected (naturally infected but not treated with Ivermectin) vs. naturally uninfected. The other factor was species. Experimental period (July vs. August) was included as a blocking factor. The dependent variable in the analysis was proportional change between pretreatment and posttreatment ADMD ([post–pre]/pre); this measure should be more sensitive than posttreatment ADMD in expressing treatment effects because it takes account of initial differences in ADMD among hosts.

TABLE 2. Effects of whipworm infection on apparent dry matter digestibility (ADMD). Standard errors are in parentheses. Figures on change between initial and final feeding trials, as well as sample sizes, are in Figure 1. See text for a description of treatments.

	Treatment		
	Deinfected	Infected	Uninfected
Dipodomys microps			
Initial ADMD	.956 (.0051)	.965 (.0029)	.955 (.0103)
Final ADMD	.961 (.0039)	.950 (.0026)	.953 (.0052)
Dipodomys ordii			
Initial ADMD	.967 (.0107)	.957 (.0076)	.961 (.0022)
Final ADMD	.955 (.0034)	.958 (.0037)	.957 (.0014)

Although there were no statistically significant main effects of treatment or species on ADMD, there was a significant interaction between these factors (Table 3), indicating that the two host species differ in their response to treatment. This difference between species was explored using a separate ANOVA for each species, which revealed that treatment with Ivermectin had a significant effect on change in ADMD in *D. microps*, but not in *D. ordii* (Table 4, Fig. 1). A Tukey's *a posteriori* multiple sample test revealed that, within *D. microps*, the change in ADMD of the deinfected group differed significantly from the change in ADMD of both the infected group and the uninfected group. These results can be interpreted as showing that the deinfected group had 1.9% higher ADMD than the other two groups.

Of interest is the lack of effect *Trichuris* causes in *D. ordii*. This may be due to what appears to be a higher intensity of infection (more parasites per infected host) in *D. microps*: fecal floats of *D. microps* in general contained more eggs than did floats of *D. ordii* (*D. microps* $\bar{X}$ = 254, SE = 115.2; *D. ordii* $\bar{X}$ = 63.5, SE = 21.0; Mann-Whitney U-test, U = 79, P = .1). If fewer worms were present in *D.*

TABLE 3. *F* values and probability values (*P*) from three-way analyses of variance on effects of species, month, and treatment (deinfected, infected, or uninfected) on apparent dry matter digestibility (ADMD).

		Dependent variable					
		Initial ADMD		Final ADMD		Proportion change in ADMD	
Source	df	*F*	*P*	*F*	*P*	*F*	*P*
Treatment	2	.15	.86	.72	.49	.47	.63
Species	1	.46	.50	.82	.37	.33	.57
Treatment * Species	2	1.33	.27	1.78	.18	4.74	.012
Block (= Month)	1	.51	.48	9.11	.003	.00	.95
Error	77						

TABLE 4. Results from one-way analyses of variance on the effect of treatment (deinfected, infected, and uninfected) on % change in dry matter digestibility in *D. microps* and *D. ordii.*

Species	Source	df	MS	*F*	*P*
D. microps					
	Treatment	2	.00106	4.64	.019
	Error	27	.000229		
D. ordii					
	Treatment	2	.00034	1.21	.31
	Error	52	.01442		

ordii, the effect of eradicating those worms would have been less apparent.

One might question the biological importance of the slight, albeit statistically significant, decrease in ADMD caused by *Trichuris* infection. Munger and Karasov (1989) showed an effect of similar magnitude resulting from tapeworm infection (*Hymenolepis citelli*) in white-footed mice (*Peromyscus leucopus*). They argued that hosts can easily compensate for such small effects by slight increases in food consumption or decreases in expenditures, or by changes in gut morphology (Mettrick 1980), and concluded that such effects on ADMD are unlikely to affect host energy budgets or to translate through to population-level effects. The same conclusion is likely to apply to the kangaroo rat–whipworm system.

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LOCAL DISTRIBUTION AND FORAGING BEHAVIOR OF THE SPOTTED BAT (*EUDERMA MACULATUM*) IN NORTHWESTERN COLORADO AND ADJACENT UTAH

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ABSTRACT.—This study investigated local distribution and foraging behavior of the spotted bat (*Euderma maculatum*) in Dinosaur National Monument, Colorado-Utah, by monitoring audible echolocation calls. The occurrence of this species was verified in a variety of habitat types in canyon bottoms and other relatively low elevation sites, indicating that the animals are widely distributed and locally common in the area. Foraging spotted bats concentrated flight activity in the open-air space above meadows and occasionally exploited near-canopy habitat (within 8 m of foliage). Bats began to forage shortly after dark, and activity levels were relatively constant throughout the night. Foraging spotted bats attacked airborne prey every 2.15 min on average. Consistent with published observations, spotted bats maintained exclusive foraging areas. Distinct vocalizations indicating agonistic encounters occurred when a bat encroached on the foraging area of a conspecific.

Key words: spotted bat, Euderma maculatum, *Colorado, Utah, Dinosaur, National Monument, foraging, habitat use, attack rates, echolocation.*

The spotted bat (*Euderma maculatum*) is widely distributed across western North America and apparently exists in low population numbers throughout its range (Fenton et al. 1987). The species is rare in collections, and viable populations have been documented in only a few widely separated localities (Watkins 1977, O'Farrell 1981). Findings presented here and those of Navo et al. (1992) indicate that *E. maculatum* is locally common in canyon bottoms and other low-elevation sites in Dinosaur National Monument, Colorado-Utah, and occurs throughout a diverse range of habitat types.

Population studies (e.g., Leonard and Fenton 1983) in south central British Columbia have demonstrated that foraging spotted bats exhibit considerable habitat specificity; radiotracking in this same area (Wai-Ping and Fenton 1989) has demonstrated that individuals are faithful to specific sites over several consecutive nights. However, no clear association between foraging activity and any specific habitat conditions is apparent. In British Columbia, spotted bats forage over clearings in ponderosa pine (*Pinus ponderosa*) forests, open fields, and marshes (Leonard and Fenton 1983, Wai-Ping and Fenton 1989). There is little information about foraging habitat throughout the remainder of the geographic range of *E. maculatum*.

The purpose of this study was (1) to investigate local distribution of *E. maculatum* by monitoring echolocation calls, (2) to identify and describe foraging habitat, and (3) to make a preliminary examination of spatial and temporal patterns of habitat use by spotted bats in the study area.

METHODS

This study was conducted in the canyon bottoms and other relatively low elevation sites in Dinosaur National Monument (109°W, 40°31′N), northwestern Colorado and northeastern Utah, from 17 May to 9 June 1993. Navo et al. (1992) provided a description of the physiography and vegetation of Dinosaur National Monument. In each study site where spotted bats occurred, I monitored movement patterns and foraging behavior by listening to the low-frequency (15–9 kHz; Leonard and Fenton 1984) echo-location calls of this species, which are clearly audible to the unaided human ear (Woodsworth et al. 1981).

As reported previously (Navo et al. 1992), *E. maculatum* is readily identifiable because it has the lowest-frequency echolocation calls of any bat species in the study area. *Nyctinomops macrotis* and *Idionycteris phyllotis* also produce orientation sounds that are partly audible to humans, with frequencies of 25–17 kHz for *N. macrotis* (Fenton and Bell 1981) and 24–12 kHz for *I. phyllotis* (Simmons and O'Farrell 1977). These two species inhabit southern parts of the Colorado Plateau and the Great Basin (Milner et al. 1990, Tumlison 1993), but neither is known to occur as far north as Dinosaur National Monument, extralimital records of *N. macrotis* notwithstanding (Milner et al. 1990). To further ensure correct call identification, I referred to recordings of known *E. maculatum* calls. I also visually identified free-flying individuals (based on conspicuous white venter and large ears) at close range in the beam of a high-intensity flashlight after locating the animals by listening to orientation sounds. It should be noted that *I. phyllotis* is often buff-colored ventrally and therefore could be visually misidentified as *E. maculatum* in areas of sympatry.

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Sampling Locations

To investigate the ecological distribution of *E. maculatum*, I sampled 15 sites at 12 locations representative of common low-elevation habitat types in the area (Fig. 1). Riparian sites (Jenny Lind Rock, 1603 m; Echo Park, 1553 m; Split Mountain Gorge, riverbank and sandbar, 1439 m) are characterized by wide channels and reaches of calm water bounded by steep sandstone cliffs. Isolated stands of boxelder (*Acer negundo*) and cottonwood (*Populus fremontii*) line the riverbanks along with thickets of tamarisk (*Tamarix* sp.).

Orchid Draw (1484 m) and Red Wash (1537 m) are dry desert washes characterized by rabbitbrush (*Chrysothamnus nauseosus*), sagebrush (*Seriphidium tridentata*), greasewood (*Sarcobatus vermiculatus*), and shadscale (*Atriplex confertifolia*), with tamarisk dominating drainage bottoms.

Echo Park Meadow (1548 m) and Pool Creek (1635 m) are both open meadows with dominant ground cover of cheatgrass (*Anisantha tectorum*), various bunchgrasses, and isolated clumps of boxelder. Echo Park Meadow encompasses an area of ca 18 ha, bounded by the Green River to the west and high (150–230 m) sandstone cliffs on remaining sides. The meadow at Pool Creek (ca 8 ha) is situated at the mouth of a narrow canyon; boxelder and cottonwood form a dense, continuous canopy over much of the adjacent creek.

Remaining locations consist of a moist meadow (Hog Canyon, 1635 m), open sagebrush shrublands (Rainbow Park, 1488 m; Island Park, 1512 m), and a narrow canyon with thick riparian vegetation (Jones Hole, 1585 m).

Sampling Methods

At all locations I remained at a single site during each night of sampling. By pacing from a boxelder, which served as a focal point of bat foraging activity in Echo Park Meadow, I estimated that calls of *E. maculatum* were detectable at a distance of roughly 100 m. Therefore, the area sampled at each site is here defined as the air space within a hemisphere of radius 100 m. On several nights periods of high wind and/or rain reduced this range of detectability, with an attendant underestimation of bat activity. Furthermore, sites differed slightly in levels of background noise from nearby streams, the amount of obstructive vegetation, and various atmospheric conditions such as relative humidity, all of which affect the propagation of sound (Lawrence and Simmons 1982).

Study sites were situated either at the mouths of canyons or draws or in the middle of open areas where movement patterns of bats could best be assessed and the range of detectability was maximized. In locations characterized by expansive terrain (open meadows or shrublands), I monitored two different sites separated by >300 m on consecutive nights to assess uniformity of activity levels over large areas. All sites were monitored from 2000 to 0200 h with the exception of Echo Park Meadow, which was monitored from 2000 to 0400 h for seven consecutive nights (19–26 May) to assess temporal patterns of foraging activity.

At locations where I observed high levels of foraging activity (e.g., Echo Park Meadow and Pool Creek), bat activity was quantified by timing the duration of individual foraging sessions and recording the number of feeding buzzes (the increased rate of echolocation pulse repetition associated with attacks on airborne prey; Griffin et al. 1960). Following Leonard and Fenton (1983), the occurrence of feeding buzzes indicates foraging activity, and a foraging session is defined as the time during which a single spotted bat hunted continuously within the study site. To permit comparison

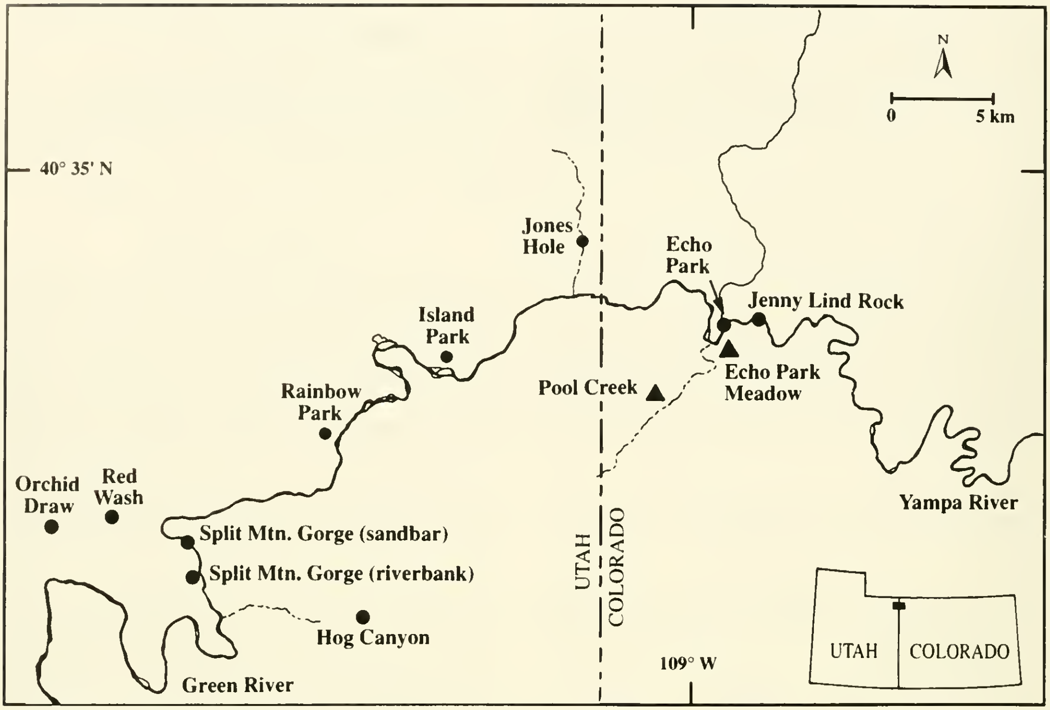

Fig. 1. Map showing sampling locations for monitoring activity of *Euderma maculatum* in Dinosaur National Monument in late spring 1993. Circles = locations at which transient occurrences of commuting or foraging bats were recorded; triangles = foraging areas (see text for details).

of relative levels of activity throughout the night, the time spent by spotted bats in the study site was totaled for every 15-min period sampled. Sampling periods during which heavy rain occurred were not considered.

To assess spatial patterns of habitat use, I described the foraging flights of spotted bats into a minicassette recorder and noted flight patterns and use of available foraging space relative to a near-canopy habitat zone (within 8 m of tree canopies) and an open-area zone (the clutter-free air space over the open meadow). These habitats correspond to habitat zones 1 and 4, respectively, proposed by Aldridge and Rautenbach (1987). I recorded the duration of foraging activity occurring within each zone as well as the number of bats simultaneously present within the study site and interactions between them.

I recorded the number of feeding buzzes heard during each foraging session for each night of observation at Echo Park Meadow and Pool Creek for the purpose of calculating attack rates (feeding buzzes/min) of foraging spotted bats. I considered only those foraging sessions of duration >3 min during which all feeding buzzes produced by a single individual within the study site could be counted accurately.

At other locations where I observed only transient occurrences of foraging or commuting spotted bats, activity was quantified by recording the number of bat passes (sensu Fenton 1970) per 15-min sampling period.

RESULTS AND DISCUSSION

I observed spotted bats in 13 of 15 sites sampled (Table 1). At 8 of these locations I observed only commuting bats. Passes of commuting spotted bats occurred sporadically throughout the night. At locations where two separate sites were monitored on consecutive nights, the number of passes remained fairly constant (passes/night: Echo Park, 5, 4; Hog Canyon, 5, 6; Island Park, 6, 10), and directions of travel appeared similar for bats on both nights.

Availability of cliff roosting sites has been suggested as a limiting factor in the distribu-

TABLE 1. Number of passes of *Euderma maculatum* per 15-min sampling period between 2000 and 0200 h at Dinosaur National Monument (16 May–8 June 1993). See text for general description of habitat types.

Sampling location	Number of nights	Number of sampling periods	n	$\bar{x}$	Range
Jenny Lind Rock	1	24	0	0	—
Echo Park	2	48	9	.19	0–2
Hog Canyon	2	48	11	.23	0–3
Orchid Draw	1	24	18	.75	0–6
Red Wash	1	24	32	1.33	0–1
Split Mountain Gorge (sandbar)	1	24	1	.04	0–5
Split Mountain Gorge (riverbank)	1	24	8	.33	0–8
Rainbow Park	1	16	4	.25	0–1
Island Park	2	48	16	.33	0–2
Jones Hole	1	24	0	0	—
All sites	13	280	99	.35	0–8

tion of *E. maculatum* (Easterla 1973). The abundance of high cliffs in Dinosaur National Monument as well as transient occurences of commuting bats throughout a variety of widely separated low-elevation sites (Navo et al. 1992, this study) suggests that suitable roosting habitat is widespread throughout the area. However, information about microclimate requirements of this species is needed to fully assess actual availability of suitable roost sites.

I observed foraging spotted bats by sight and sound at five locations, three of which (Echo Park, Orchid Draw, Red Wash) involved only transient occurrences of bats that were observed executing steep dives and other abrupt flight maneuvers coincident with feeding buzzes as they passed through the area. I observed a single spotted bat foraging over a sand-and-gravel bar at Echo Park, but activity levels at this location were lower than those reported by Navo et al. (1992), who sampled this same site previously. Fairly high levels of activity occurred at Orchid Draw and Red Wash (Table 1), and I heard three feeding buzzes at each site. However, because spotted bats apparently capture prey opportunistically while commuting to specific foraging sites (Wai-Ping and Fenton 1989), observations of foraging bats passing through an area cannot be considered indicative of habitat preferences.

At Echo Park Meadow, spotted bats first arrived at the study site at 2123 h ± 11 min Mountain Daylight Time (n = 6 rain-free evenings), always after dark, and remained active throughout the night (Fig. 2). Spotted bats foraged within the study site for 6.22 ± 2.40 min out of every 15-min sampling period between 2100 and 0400 h (n = 2490 min; Fig. 2), and foraging sessions lasted 5.48 ± 2.74 min (n = 187). At Pool Creek, spotted bats hunted within the study site for 6.82 ± 5.03 min out of every 15-min sampling period between 2100 and 0200 h (n = 525 min), and foraging sessions lasted 8.97 ± 8.78 min (n = 30). These activity levels offer strong evidence that open meadows represent important foraging habitat for *E. maculatum* in this area.

Comparatively low levels of activity were recorded at riparian sites adjacent to Echo Park Meadow (Echo Park, Jenny Lind Rock). Because no physiographic barriers are present that might restrict accessibility to the bats, it appears that open water courses do not represent foraging areas of choice. These observations agree with those of Leonard and Fenton (1983), who reported that in British Columbia spotted bats foraged in forest clearings and open fields to the exclusion of a nearby river.

The temporal pattern of foraging activity in Dinosaur National Monument is similar to that reported from British Columbia (Leonard and Fenton 1983), where spotted bats were active throughout the night. Because radiotracking (Wai-Ping and Fenton 1989) has demonstrated that individual spotted bats hunt on the wing >300 min per night, reports of apparent peaks in nightly activity (which have been especially pronounced in mistnetting studies, e.g., Easterla 1973) are likely artifacts related to the proximity of sampling sites to diurnal roosts and/or drinking sites.

At Echo Park Meadow and Pool Creek, foraging spotted bats typically flew in large circular or elliptical orbits at heights of 10–30 m above the ground. In 1088.8 min of observation of foraging spotted bats at Echo Park

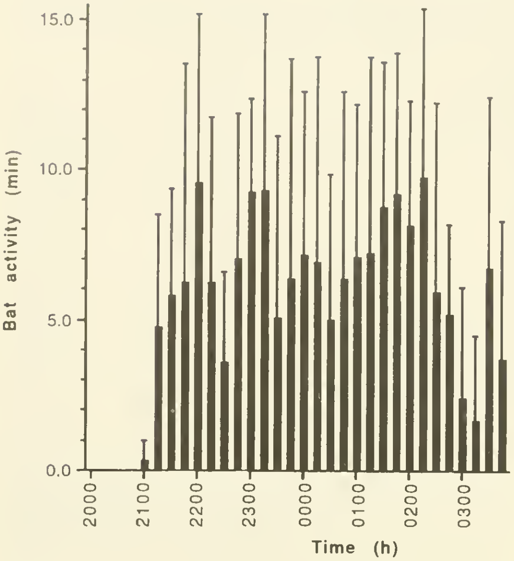

Fig. 2. Foraging activity patterns of *Euderma maculatum* at Echo Park Meadow (19–26 May 1993). Bars represent mean time (+ SD) spent by bats in the study site per 15-min sampling period from 2000 to 0400 h (n = 6 for each 15-min period in the interval 2000–0345 h, n = 4 for 0345–0400 h).

Meadow, 81.5% of activity occurred over the open meadow, which constituted roughly 85% of the site, while 18.5% of activity occurred within 8 m of the foliage of fully leafed boxelders at mid- to upper-canopy level. Such activity consisted of bats circling closely above and around individual trees or isolated clumps of trees. I rarely observed bats within 0.5 m of the canopy, and I never observed hovering flight or other evidence of foliage gleaning. In 290.8 min of observation of foraging spotted bats at Pool Creek, all activity occurred over the open meadow, although a much larger percentage of the study site area comprised canopies of boxelder and cottonwood than at Echo Park Meadow.

The predilection of *E. maculatum* for foraging over open terrain in Dinosaur National Monument agrees with the pattern observed in previous studies (e.g., Woodsworth et al. 1981, Leonard and Fenton 1983). Low-frequency echolocation calls and long intercall intervals suggest that spotted bats use a foraging strategy based on long-range prey detection and high-level flight (Simmons and Stein 1980, Woodsworth et al. 1981, Barclay 1986). This strategy likely is best suited to open areas (Neuweiler 1984). Although I never directly observed these bats gleaning prey from foliage during this study, observations of near-canopy foraging contrast with those of some other workers (e.g., Wai-Ping and Fenton 1989) who have reported that this species never attacked insects near foliage or any other type of surface. Information about individual variability in foraging behavior is needed before drawing conclusions about variability between populations related to different ecological conditions.

At both Echo Park Meadow and Pool Creek, there were 118 instances in which two or three *E. maculatum* were present within the study site simultaneously. Leonard and Fenton (1983, 1984) estimated that spotted bats in British Columbia maintain a distance of at least 50 m between adjoining foraging areas and suggested that this spacing is accomplished through a combination of mutual avoidance and active monitoring of encroachments by conspecifics. This same system appears to be operating at foraging areas in Dinosaur National Monument. Consistent with observations of Leonard and Fenton (1983), foraging spotted bats often produced agonistic vocalizations when the 50-m buffer zone was breached by an intruding bat. Such vocalizations sounded qualitatively different from feeding buzzes and occurred only during close-range encounters between conspecifics. Information about known individuals and resource availability is needed to elucidate the role of agonistic interactions in the foraging ecology of *E. maculatum*.

During this study I heard a total of 247 feeding buzzes, and never more than one per min from the same individual. In a sample of 37 foraging sessions, spotted bats attacked an insect every 2.15 min on average (0.466 ± 0.294 attacks/min, range 0.16–0.94; n = 152 feeding buzzes). These rates generally agree with values reported in previous studies (Leonard and Fenton 1983, Wai-Ping and Fenton 1989), further confirmation that this species attacks prey at a rate much lower than is typical of bats that forage from continuous flight (Barclay 1985, Hickey and Fenton 1990).

Density of clutter in an environment imposes differential constraints on the maneuverability and perceptual capacities of bats, thereby determining the accessibility of different habitats by influencing foraging efficiency (Neuweiler 1984, Aldridge and Rautenbach 1987, Fenton 1990). Spotted bats appear to forage preferentially in open areas, which may be related to the use of a long-range foraging strategy (Barclay 1986), and the ability to exploit edge situations may reflect a measure of behavioral flexibility in this regard. Because spotted bats are obviously not greatly restricted in foraging habitat with regard to vegetation associations (Wai-Ping and Fenton 1989, Navo et al. 1992), structural features of the environment related to density of clutter may be more predictive of habitat suitability and the use of available foraging space. However, information on individual variability is needed before drawing conclusions about the foraging strategy of this species.

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THE *CHRYSOTHAMNUS-ERICAMERIA* CONNECTION (ASTERACEAE)

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ABSTRACT.—The genus *Chrysothamnus* (Asteraceae) contains 16 species. Recently, 4 species were transferred to *Ericameria*, and the remaining 12 were left in *Chrysothamnus*. The remaining species are now transferred to *Ericameria* as *E. albida*, *E. depressa*, *E. eremobia*, *E. graminea*, *E. filifolia* (formerly *C. greenei*), *E. humilis*, *E. linifolia*, *E. molesta*, *E. pulchella*, *E. pulchelloides* (a fossil species), *E. spathulata*, *E. vaseyi*, and *E. viscidiflora*. Section alignments are given, and some infraspecific combinations are also made.

Key words: Chrysothamnus, Ericameria, *rabbitbrush, nomenclature transfers.*

The Asteraceae are a relatively young group, and yet they have experienced rapid evolution into a great number of species. One result is that many taxa appear more distant morphologically (phenotypically) than they actually are genetically, and, conversely, some taxa may appear more closely related than they are. These situations have created havoc amongst taxonomists in their attempts to circumscribe genera. This is particularly evident in the tribe Astereae. In 1894, E. L. Greene stated:

> In North America the Astereae are excessively numerous, and no natural assemblage of plants has seemed to present such difficulties to the systematist; and the widest conceivable diversities of opinion as to the limits of genera have found expression among botanists when undertaking to classify them.

The situation continues a century later.

The genus *Haplopappus* was thought to be an unnatural, polyphyletic assemblage by many (e.g., Shinners 1950, Anderson 1966, Johnston 1970, Turner and Sanderson 1971, Clark 1977, Urbatsch 1978). Nevertheless, because there was no suitable taxonomic reorganization of the group, I continued to describe new taxa in *Haplopappus* (Anderson 1980a, 1983b), even though the species would probably be placed in some other genera at a later date. Recently, additional data have contributed to a clearer understanding of the relationships in this and related groups (Morgan and Simpson 1992), and several genera have been recognized for North American Haplopappi.

In a 1976 presentation at national meetings, I discussed the close affinity of *Chrysothamnus* with woody elements of *Haplopappus* and suggested that the *Asiris-Ericameria-Macronema* complex of *Haplopappus* probably should be included in *Chrysothamnus*. But, given the state of knowledge at that time, I deferred. In 1990, Nesom reorganized *Ericameria* as a genus to include *Asiris* and *Macronema*. Recently, based on occurrences of intergeneric hybrids (Anderson and Reveal 1966, Anderson 1970) and DNA data (Morgan and Simpson 1992), Nesom and Baird (1993) transferred four species of *Chrysothamnus* into *Ericameria* (*C. nauseosus* and *C. parryi* of section *Nauseosi* and *C. paniculatus* and *C. teretifolius* of section *Punctati*). They continued to recognize *Chrysothamnus* as a distinct (but smaller) genus and gave arguments for separating the two.

A problem in separating *Ericameria* and *Chrysothamnus* (sensu Nesom and Baird) is the occurrence of hybrids (Anderson 1970, 1973) between *C. nauseosus* (their *Ericameria*) and *C. albidus* (their *Chrysothamnus*). After studying a specimen of only one of the three collections involved, Nesom and Baird (1993) devalued the connection by stating that "the plant in question [is] characteristic of *C. nauseosus*, and we identify it as *C. nauseosus*, finding no strong reason to implicate *C. albidus* in its parentage." They stated that achenes of *C. albidus* are linear and consistently producing 10 slightly raised nerves, whereas those of *C. nauseosus* are narrowly obovate with 5–7 nerves. Actually, achenes of both species can be characterized as being narrowly cylindrical. The number of vascular bundles (associated with the nerves) in the achenes averages approximately 7 and ranges from 5 to 10 (but mostly 6–8 in Ash Meadows) for *C. albidus* (Anderson 1970, 1973), whereas achene bundle number in *C. nauseosus* ranges from 5 to 12 (but is restricted to 5 for those in Ash Meadows).

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The interspecific hybrid examined by Nesom and Baird (*Beatley 11894*, KSC) was studied anatomically by Anderson (1973); its hybridity is indicated by low pollen fertility and by morphological intermediacy between the two species in its revolute leaves, in vascular bundle number in the ovary wall, in corolla lobe length, and in anther appendage length. It has secretory canals in the ovary wall and glandular trichomes on the corolla tube (like *C. nauseosus*, unlike *C. albidus*) and ovary wall (unlike *C. nauseosus*, like *C. albidus*). Further, progeny from one of my *C. albidus* garden plants also has low pollen fertility and looks intermediate between its seed parent and *C. nauseosus* (Anderson 1970). Its flowers have secretory canals in the ovary wall and glandular trichomes on the corolla tube but lack glandular trichomes on the ovary wall; those three features are characteristic of *C. nauseosus* but not of *C. albidus* (the seed parent), clearly suggesting hybridity. If existence of interspecific hybrids is used to justify transferring *C. nauseosus* to *Ericameria*, then this feature also argues for bringing the remainder of *Chrysothamnus* into *Ericameria*.

The warranted position of *Chrysothamnus teretifolius* in *Ericameria* is taken by Nesom and Baird (1993: 80) because, like many *Ericameria* species (sensu strictum), that species has the tendency for the "resiniferous ducts that are almost always distinctly associated with the phyllary midvein to expand near the apex of the phyllary." This characteristic also occurs in many species of *Chrysothamnus* (sensu Nesom and Baird) as illustrated for *C. vaseyi* (Anderson 1963: 660) and cannot be used to distinguish the two groups. I have observed adjacent populations of *C. viscidiflorus* subsp. *puberulus* in which plants of one had prominently enlarged resin ducts at the phyllary tips and plants of the other did not.

With the transferral of four species from *Chrysothamnus* to *Ericameria*, Nesom and Baird (1993) separate the two newly structured genera with six criteria. (1) Leaves 3-nerved for *Chrysothamnus* and 1-nerved for *Ericameria*—but many of their *Ericameria* have prominently 3-nerved leaves. Hall and Clements (1923) used nerve number to distinguish *C. nauseosus* ssp. *graveolens* from spp. *consimilis* (so the character is variable even within a species). Many of the latter group, such as *C. albidus*, *C. greenei*, and some forms of *C. viscidiflorus*, appear to have 1-nerved leaves. Actually, all species of *Ericameria* and *Chrysothamnus* have trilacunar, 3-trace nodal anatomy (personal observation); thus, the character of 1 versus 3 nerves is a matter of perception, not of fact. (2) Leaf margins ciliate in the former and never in the latter—but *C. albidus*, *C. eremobius*, and *C. viscidiflorus* subsp. *planifolius* of the former have entire leaf margins; also in that group, *C. pulchellus* subsp. *pulchellus* has entire leaf margins, whereas subsp. *baileyi* has ciliate leaf margins, and some populations of *C. gramineus* and *C. vaseyi* have entire leaf margins, but others do not. *Ericameria* (sensu Nesom 1990) has several species that have leaves with ciliate leaf margins, fairly prominent in *E. cooperi* and less so in several other species (e.g., *E. cervina*, *E. nana*, *E. ophitidis*, and *E. zionis*). (3) Corollas more or less abruptly broadened from the tube into the throat with long, recurving or coiling lobes in the former and corollas tubular with short, erect or spreading lobes in the latter—but corollas of *C. spathulatus* (of the latter) have relatively broad tubes that lack noticeably flaring throats, *C. humilis* (of the former) has tubular corollas with short, erect lobes (Anderson 1964: 226), and *C. nauseosus* ssp. *ceruminosus* (of the latter) has corollas that are abruptly broadened from the tube into the throat with long, spreading lobes. (4) Style appendage collecting hairs merely papillate in the former, whereas they are long and sweeping in the latter—but *C. albidus*, *C. molestus*, *C. pulchellus*, and certain populations of *C. viscidiflorus* (all of the former) have style appendages with moderately long, sweeping hairs. Diversity in collecting hairs is greater in *Chrysothamnus* (sensu Anderson 1986) than Nesom and Baird (1993) imply and does not fall into two groups. Collecting hair length may be correlated with other floral features; namely, the corollas, style lengths, and pollen volumes of the former group (Anderson 1966) are generally smaller than those of the latter. (5) Involucral bracts in vertical files in the former (caveat noted) and usually not in vertical files in the latter—but, perhaps the most strongly aligned bracts occur in *C. nauseosus* ssp. *arenarius* (of the latter). (6) Achenes glandular with nonresinous nerves in the former and eglandular (with duplex hairs) and resinous nerves in the latter—but only five species of the former have glandular achenes (in some they are hidden by duplex hairs) and the other seven do not, having either glabrous achenes or achenes with duplex hairs exclusively (Anderson 1970, 1983a), and many have resin canals associated with the bundles of the achenes, admittedly fewer than in those of the latter but well developed in *C. molestus* of the former. Also, *C. paniculatus* (of the latter grouping) lacks resin canals in its achenes (Anderson 1970). None of these six sets of characteristics can be used to consistently separate the two groups.

Clearly, *Chrysothamnus* (sensu Anderson 1986, not Nesom and Baird 1993) is fairly homogeneous and should not be dismembered. If some are to go into *Ericameria* (and DNA data suggest they should), then all should go into *Ericameria*. Therefore, the remaining 12 species of *Chrysothamnus* are transferred to *Ericameria*, and new combinations are made here.

1. **Ericameria albida (M. E. Jones ex A. Gray) L. C. Anders., *comb. nov.*** Basionym: *Bigelovia albida* M. E. Jones ex A. Gray, Proc. Amer. Acad. Arts 17: 209. 1882. *Chrysothamnus albidus* (M. E. Jones ex A. Gray) E. Greene, Erythea 3: 107. 1895.

2. **Ericameria depressa (Nutt.) L. C. Anders., *comb. nov.*** Basionym: *Chrysothamnus depressus* Nutt., Proc. Acad. Nat. Sci. Philadelphia 4: 19. 1948. *Linosyris depressa* (Nutt.) Torr., in Stigreaves, Rept. Exped. Zuni & Colorado Rivers 161. 1853. *Bigelovia depressa* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 8: 643. 1873.

3. **Ericameria eremobia (L. C. Anders.) L. C. Anders., *comb. nov.*** Basionym: *Chrysothamnus eremobius* L. C. Anders., Brittonia 35: 23. 1983.

4. **Ericameria graminea (H. M. Hall) L. C. Anders., *comb. nov.*** Basionym: *Chrysothamnus gramineus* H. M. Hall, Muhlenbergia 2: 342. 1916. *Petradoria discoidea* L. C. Anders., Trans. Kansas Acad. Sci. 66: 676. 1964.

5. **Ericameria filifolia (Rydb.) L. C. Anders. *comb. nov.*** Basionym: *Chrysothamnus filifolius* Rydb., Bull. Torrey Bot. Club 28: 503. 1901. *Bigelovia greenei* A. Gray, Proc. Amer. Acad. Arts 11: 75. 1876 [not *Ericameria greenei* (A. Gray) Nesom]. *Chrysothamnus greenei* (A. Gray) E. Greene, Erythea 3: 94. 1895. *Chrysothamnus pumilus* var. *acuminatus* A. Nels., Bot. Gaz. 28: 376. 1899. *Chrysothamnus scoparius* Rydb., Bull. Torrey Bot. Club 28: 504. 1901. *Chrysothamnus laricinus* E. Greene, Pittonia 5: 110. 1903.

6. **Ericameria humilis (E. Greene) L. C. Anders., *comb. nov.*** Basionym: *Chrysothamnus humilis* E. Greene, Pittonia 3: 24. 1896.

7. **Ericameria linifolia (E. Greene) L. C. Anders., *comb. nov.*** Basionym: *Chrysothamnus linifolius* E. Greene, Pittonia 3: 24. 1896.

8. **Ericameria molesta (Blake) L. C. Anders., *comb. nov.*** Basionym: *Chrysothamnus viscidiflorus* var. *molestus* Blake, J. Wash. Acad. Sci. 30: 368. 1940. *Chrysothamnus molestus* (Blake) L. C. Anders., Madroño 17: 222. 1964.

9a. **Ericameria pulchella (Gray) L. C. Anders., *comb. nov.*** Basionym: *Linosyris pulchella* A. Gray, Pl. Wright. [Smiths. Contr. Knowl.] 3(5): 96. 1856. *Bigelovia pulchella* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 8: 643. 1873. *Chrysothamnus pulchellus* (A. Gray) E. Greene, Erythea 3: 107. 1895.

9b. **Ericameria pulchella subsp. baileyi (Woot. & Standl.) L. C. Anders., *comb. nov.*** Basionym: *Chrysothamnus baileyi* Woot. & Standl., Contr. U.S. Natl. Herb. 18: 181. 1913.

9c. **Ericameria pulchella subsp. pulchella var. elatior (Standl.) L. C. Anders., *comb. nov.*** Basionym: *Chrysothamnus elatior* Standl., Proc. Biol. Soc. Wash. 26: 118. 1913. This variety with uniformly pubescent leaves occurs sporadically in a few populations of the typically glabrous-leaved subspecies *pulchellus* and does not warrant a higher taxonomic status than this quadrinomial affords.

10. **Ericameria spathulata (L. C. Anders.) L. C. Anders., *comb. nov.*** Basionym: *Chrysothamnus spathulatus* L. C. Anders., Madroño 17: 226. 1964. *Chrysothamnus viscidiflorus* var. *ludens* Shinners, Sida 1: 374. 1964.

11. **Ericameria vaseyi (A. Gray) L. C. Anders., *comb. nov.*** Basionym: *Bigelovia vaseyi* A. Gray, Proc. Amer. Acad. Arts 12: 58. 1876. *Chrysothamnus vaseyi* (A. Gray) E. Greene, Erythea 3: 96. 1895. *Chrysothamnus bakeri* E. Greene, Pittonia 4: 152. 1900.

12a. **Ericameria viscidiflora (Hook.) L. C. Anders. *comb. nov.*** Basionym: *Crinitaria viscidiflora* Hook., Fl. Bor. Am. 2: 24. 1834. *Chrysothamnus viscidiflorus* (Hook.) Nutt. Trans. Amer. Philos. Soc. 11, 7: 324. 1840. *Bigelovia douglasii* A. Gray, Proc. Amer. Acad. Arts 8: 645. 1873. *Chrysothamnus douglasii* (A. Gray) Clements & Clements, Rocky Mtn. Fls. 226. 1914. *Chrysothamnus pumilus* Nutt., Trans. Amer. Philos. Soc. 11, 7: 323. 1840. *Linosyris serrulata* Torr., Stansbury Rep. 1: 389. 1851. *Chrysothamnus serrulatus* (Torr.) Rydb., Bull. Torrey Bot. Club 33: 152. 1906. *Chrysothamnus tortifolius* E. Greene, Fl. Fran. 368. 1897. *Chrysothamnus leucocladus* E. Greene, Pittonia 5: 59. 1902. *Chrysothamnus stenolepis* Rydb., Bull. Torrey Bot. Club 37: 131. 1910.

12b. **Ericameria viscidiflora subsp. viscidiflora var. latifolia (D. C. Eaton) L. C. Anders., *comb. nov.*** Basionym: *Linosyris viscidiflora* var. *latifolia*

D. C. Eaton, Bot. King Expl. 157. 1871. *Chrysothamnus latifolius* (D. C. Eaton) Rydb., Bull. Torrey Bot. Club 33: 152. 1906.

12c. *Ericameria viscidiflora* subsp. *viscidiflora* var. *stenophylla* (A. Gray) L. C. Anders., *comb. nov.* Basionym: *Bigelovia douglasii* var. *stenophylla* A. Gray, Proc. Amer. Acad. Arts 8: 646. 1873. *Chrysothamnus stenophyllus* (A. Gray) E. Greene, Erythea 3: 94. 1895. These quadrinomials (12b and 12c) identify sporadic but rather distinctive morphotypes that occur in the northern regions of this subspecies (for conceptual distinction between subspecies and variety, see Anderson 1980b)

12d. *Ericameria viscidiflora* subsp. *axillaris* (Keck) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus axillaris* Keck, Aliso 4: 104. 1958.

12e. *Ericameria viscidiflora* subsp. *lanceolata* (Nutt.) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus lanceolatus* Nutt., Trans. Amer. Philos. Soc. II, 7: 324. 1840. *Chrysothamnus elegans* E. Greene, Erythea 3: 94. 1895. *Bigelovia douglasii* var. *spathulata* Jones, Proc. Calif. Acad. Sci. II 5: 690. 1895. *Chrysothamnus glaucus* A. Nels., Bull. Torrey Bot. Club 25: 377. 1898. *Chrysothamnus pumilus* var. *latus* A. Nels., Bot. Gaz. 54: 413. 1912.

12f. *Ericameria viscidiflora* subsp. *planifolia* (L. C. Anders.) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus viscidiflorus* subsp. *planifolius* L. C. Anders., Madroño 17: 223. 1964.

12g. *Ericameria viscidiflora* subsp. *puberula* (D. C. Eaton) L. C. Anders., *comb. nov.* Basionym: *Linosyris viscidiflora* var. *puberula* D. C. Eaton, Bot. King Expl. 158. 1871. *Chrysothamnus puberulus* (D. C. Eaton) E. Greene, Erythea 3: 93. 1895. *Chrysothamnus marianus* Rydb., Bull. Torrey Bot. Club 37: 131. 1910.

The following sections in *Ericameria* are proposed to accommodate these species transfers: *Ericameria* section *Chrysothamnus* (A. Gray) L. C. Anders., *comb. nov.* Basionym: *Bigelovia* section *Chrysothamnus* A. Gray., Proc. Amer. Acad. Arts 8: 641. 1873. This section includes *E. albida, E. filifolia, E. humilis, E. linifolia, E. spathulata,* and *E. viscidiflora. Ericameria* section *Gramini* (L. C. Anders.) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus* section *Gramini* L. C. Anders., Proc. Symp. Biology of *Artemisia* and *Chrysothamnus* 29. 1986. This section includes *E. eremobia* and *E. graminea. Ericameria* section *Pulchelli* (Hall & Clements) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus* section *Pulchelli* Hall & Clements, Carnegie Inst. Publ. 326: 175, 193. 1923. This section includes *E. depressa, E. molesta, E. pulchella,* and *E. vaseyi.*

Additionally, there is a fossil species, *Ericameria pulchelloides* (L. C. Anders.) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus pulchelloides* L. C. Anders., Great Basin Naturalist 40: 351. 1980.

Nesom and Baird (1993) suggest the *Chrysothamnus* taxa that I have just transferred to *Ericameria* should be placed in a restructured genus to include elements of *Hesperodoria, Petradoria,* and *Vanclevea.* They conclude that chloroplast DNA data (Suh 1989) show *Petradoria* to be integrally related to the *Solidago* lineage and far removed from *Ericameria.* However, they note that neither Suh (1989) nor Morgan and Simpson (1992) sampled any taxa of *Chrysothamnus* sensu Nesom and Baird. These taxa need DNA profiles determined because they certainly do not make a morphologically compatible grouping with *Petradoria* or *Vanclevea.* For example, *Petradoria* (Anderson 1963) has radiate heads with disk flowers that lack stigmatic areas on the style branches and have abortive ovaries, and *Vanclevea* (Anderson and Weberg 1974) has large turbinate heads with many phyllaries, many flowers, and a tardily deciduous pappus of paleacous awns—none of these conditions are found in *Chrysothamnus* sensu Nesom and Baird. The cohesiveness of *Chrysothamnus* sensu Anderson is further illustrated in that *C. spathulatus* twigs emit odor similar to that of *C. nauseosus* (Anderson 1964: 227).

Two alternate taxonomies are now available: one for *Chrysothamnus* as a genus (Anderson 1986) or as a component of *Ericameria* (Nesom and Baird 1993, and here); both are preferable to merging some elements of *Chrysothamnus* with *Petradoria* or *Vanclevea.*

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REPRODUCTIVE BEHAVIOR IN MERRIAM'S CHIPMUNK (*TAMIAS MERRIAMI*)

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Key words: Tamias, Eutamias, Neotamias, *chipmunk, copulation, olfaction.*

The literature contains little information regarding mating chases and copulation in any of the western chipmunks (*Tamias*, subgenus *Neotamias*). Callahan (1981) reported mating chases for Merriam's (*T. merriami*) and dusky chipmunks (*T. obscurus*), but noted (unpublished) that both copulating pairs were partly concealed by foliage. Larson (1981) described two copulations for Merriam's chipmunk, but a careful reading suggests that one of these was a mounting attempt by an immature male and the other was observed from a considerable distance. Best and Granai (1994) found no references on this subject other than Callahan (1981) and Larson (1981).

There has been some speculation and difference of opinion regarding reproductive isolating mechanisms in parapatric species of western chipmunks. Blankenship and Brand (1987) reported differences in vocal behavior between *Tamias merriami* and *T. obscurus* at Black Mountain (Riverside County, CA) and noted a possible role in reproductive isolation. One of us (JRC), however, had previously conducted a more extensive study of vocal behavior in these two cryptic species at Black Mountain from 1975 to 1980. Vocalizing individuals were collected to confirm species identity, and sonograms were prepared and measured; yet no statistically significant vocal differences were found (Callahan 1981, and in preparation). Ecological, olfactory, and mechanical barriers to hybridization also have been suggested (Callahan 1977, 1981, Patterson 1984). These hypotheses cannot be tested without more data on chipmunk reproductive behavior. Accordingly, this note provides the first detailed description of western chipmunk copulation that has been published, to the best of our knowledge. Comparative data for other western chipmunk species would be of interest.

The observation was made 1 April 1994 in a wooded residential area in Idyllwild, Riverside County, CA (elevation 1590 m), between 1000 and 1130 h. The habitat is mixed-conifer forest dominated by incense cedar (*Calocedrus decurrens*), yellow pine (*Pinus ponderosa*), live oak (*Quercus chrysolepis*), and black oak (*Q. kelloggii*), with a sparse understory of chaparral shrubs. When the observer arrived at 1000 h, six to seven Merriam's chipmunks, many of them males, were running over, around, and through a large woodpile while performing conspicuous leaping maneuvers. No agonistic interaction was observed. It was not possible at this stage to identify the female(s) or to tell in which direction the "chase" was headed. The overall effect was somewhere between a *Sciurus*-like mating chase (e.g., Thompson 1977), in which several males follow one female, and a lek, involving male display. The chase covered an area 13–15 m in diameter but centered on the woodpile and a nearby heap of smaller pine branches.

After about 20 min, one chipmunk (later identified as female) ran up on one of the piled branches. A second chipmunk approached and they ran around for a few seconds. The female stopped on a branch and the other chipmunk, a male, ran up beside her. His entire right side was in contact with her left side for about 1 sec, during which he made a nuzzling motion with the right side of his face on the rear left portion of her face. The expected nasal/genital contact was not observed, but the pair had been out of sight for a short time previously and this could have occurred. The female then jumped to another branch, which was 5 cm in diameter and 20 cm above the ground, sloping at a 25° angle so that the female was facing downhill. Copulation then occurred only 2 m from the observer (who was inside a parked vehicle).

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The female crouched on the branch as if resting. The male jumped to that branch and quickly grasped the female from the rear with his forelimbs around her pectoral region. The female's tail was deflected to the side and slightly raised, and the male's tail was extended to the rear. Copulation consisted of four series of pelvic thrusts. Each series (except the last) lasted about 4 sec and comprised an estimated 12–24 thrusts, at a rate of 3–6 per sec. Each series of rapid thrusts was followed by a short resting period, during which the male stopped thrusting and brushed his face (mouth, nose, and chin) from side to side 2–4 times against the back of the female's neck. The fourth and last series of thrusts was shorter than the first three. The male then released his grip on the female, dismounted, and ran off into the woodpile. The female, who had remained motionless during the act, remained on the branch about 1 sec and then also ran to the woodpile. The entire copulation lasted about 18 sec.

Although several male chipmunks participated in the chase, none of them approached the copulating pair. No chipmunks were heard vocalizing during the mating chase or copulation. We did not note any pre-mating vocal display or *Lockrufe* by the estrous female (Callahan 1981), but we were not present on the days when the display (if any) would have taken place. The *Tamias* vocal display has been reported for a few species of chipmunks by Callahan (1981), Blake (1992), and others. It is not clear whether this vocal display is universal or occurs only at low population densities, when the female benefits by attracting more distant males.

No further copulations were seen, but as many as seven male chipmunks continued to run around the same woodpile for another hour. The level of activity appeared to decrease, and there were none of the prodigious leaps seen earlier. The group then gradually dispersed as individuals headed for an adjacent area where other chipmunks were heard giving occasional "chipper" vocalizations (not the long series of chips that characterizes the *Lockrufe*).

The behavior described above suggests that scent glands play a key role in reproductive behavior of this species. Larson (1981) and others have noted that male chipmunks have scent glands near the chin and angle of the jaw (oral glands) that become enlarged during the breeding season. Scent marking is prevalent in sciurids, but usually this means marking the ground or a branch, not marking another animal. The "nuzzling" and "brushing" behavior of the male Merriam's chipmunk, before and during copulation, suggests that he was scent marking the female.

Conspecific marking has been described for various mammals, such as rabbits (Mykytowycz 1965), but not for sciurids. Gurnell (1987) describes "face-wiping" behavior by various tree squirrels, but only in the context of substrate marking and (in *Paraxerus*) self-grooming; his description of copulation in *Sciurus* and *Tamiasciurus* says nothing about the male marking the female. With reference to olfactory communication in ground squirrels, Halpin (1984) wrote that "there is no experimental evidence that conspecific marking . . . actually occur[s] among the sciurids."

Our observation indicates that conspecific marking does occur in Merriam's chipmunk as a component of reproductive behavior. Without experimental data, it is not possible to determine the significance of this marking. Pair bonding comes to mind, but there is no good evidence of long-term pair bonding in Merriam's or any other species of western chipmunk, despite many years of field observation. Other possibilities include the following: (1) the marking induces some required physiological state in the female; (2) the marking tells other males that the female has already mated (before the copulation plug forms and the message becomes redundant); or (3) the marking reinforces a short-term pair bond to ensure that subsequent copulations (if any) on the day of estrus will be with the same male. Larson (1981) indicated that the same estrous female sometimes copulates more than once.

Mortality from all causes is higher for male than for female chipmunks (Smith 1978), perhaps due in part to the dispersal and exposure associated with the breeding season (Callahan 1981). After incurring the risk of predation and expending considerable energy on the mating chase, it should be to the male's advantage to ensure that his genes are passed to all the female's offspring of the season.

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ADDITIONAL RECORDS OF FLEAS (SIPHONAPTERA) FROM UTAH

James R. Kucera[1]

Key words: Siphonaptera, fleas, Utah, Megabothris asio megacolpus, Euhoplopsyllus glacialis lynx.

Subsequent to the important work of Stark (1959), few publications have given flea collection records from Utah. These include Jellison and Senger (1976) and Kucera and Haas (1992); but most effort in this area has been that of Egoscue (1966, 1976, 1977, 1988, 1989).

Herein is presented information for 10 species of Siphonaptera for Utah. A number of important records were obtained from the flea collection at the Monte L. Bean (MLB) Life Science Museum, Brigham Young University, Provo, UT. Catalog numbers of host specimens deposited in the University of Utah Museum of Natural History (UU) mammal collection and flea specimens in the MLB Museum (BYU) insect collection are given in parentheses when available. Unless indicated otherwise, specimens were collected by me and are retained in my personal collection.

Carteretta clavata Good 1942

Washington Co.: west slope Beaver Dam Mts., vic. Welcome Spring, 1220 m, 20 March 1988, 1♀ ex *Chaetodipus formosus.* "Beaver Dam," 23 February 1952, 1♀ (BYU #3462) ex *Perognathus* [=*Chaetodipus*] *formosus,* coll. C. L. Hayward. Beaver Dam Wash, 17 April 1952, 1♂ (BYU #3607) ex *Peromyscus truei,* coll. Grace Grant et al.

Few collections of this species are known from Utah (Tooele County: Stark 1959 [1♂], Egoscue 1976 [1 specimen, sex unknown]; Washington County: Jellison and Senger 1976 [2♂♂, 2♀♀]). It has also been collected in Clark County, NV (the type locality, Good 1942), and Mohave County, AZ (Augustson and Durham 1961). It is likely a nest flea of *C. formosus.*

Nearctopsylla brooksi (Rothschild 1904)

Utah Co.: Provo, 21 August 1951; 1♂, 1♀ (BYU #1366 & 1365) ex *Mustela frenata,* coll. D. Brown. Provo Canyon, 16 June 1959; 2♂♂, 7♀♀ ex *Spilogale gracilis,* coll. D E. Beck.

This species was previously known in Utah from a single collection in Sevier County (Stark 1959). It is usually found on weasels (*Mustela* spp.).

Nearctopsylla hyrtaci (Rothschild 1904)

Salt Lake Co.: Wasatch Mts., Big Cottonwood Canyon, vic. Redman campground, 2560 m (spruce-fir), 21 October 1990, 1♀ ex *Sorex monticolus* (UU #29163). Same locality, 28 October 1990, 1♀ ex *Sorex monticolus* (UU #29164).

Stark (1959) reported this species from Cache County. My collections extend the known range of this species further south in Utah along the Wasatch Cordillera. It is found on shrews (*Sorex* spp.) and *Mustela* spp.

Delotelis telegoni (Rothschild 1905)

Salt Lake Co.: Wasatch Mts., Big Cottonwood Canyon, vic. Redman campground, 2560 m (spruce-fir), 21 October 1990, 1♂ ex *Clethrionomys gapperi.* Same date & locality, 1♀ ex *Tamiasciurus hudsonicus* nest. [The nest, about 3 m above ground level, also contained many red squirrel fleas (*Orchopeas c. caedens*). The squirrel probably carried this vole flea to its nest.] Same locality, 15 September 1991, 1♀ ex *Peromyscus maniculatus.* Same locality, 5 October 1991, 1♂ ex *Clethrionomys gapperi.*

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Delotelis telegoni has rarely been found in Utah; single specimens have been collected in Sanpete County (Stark 1959) and in Utah County (Egoscue 1988). It is significant that these collections were made in summer months (August 1951 and July 1985, respectively). Many more collections will likely be made if this species is searched for during the cooler months of the year. Also, it presumably would be profitable to search nests of *Microtus* and *Clethrionomys* for this species.

Meringis shannoni (Jordan 1929)

Eads et al. (1987) listed two collections of this species from Utah. The specimens are present in the BYU collection. However, the records are erroneous because the collection locality (Douglas County) does not exist in Utah. All other cited records of this species are from the states of Washington and Oregon, except a lone locality record in Humboldt County, NV (Lewis et al. 1988).

Stenistomera hubbardi
Egoscue 1968

This rare species was listed by Tipton and Saunders (1971) as occurring in Utah although no specific records were cited. Egoscue (personal communication) knows of no records from Utah, and no specimens were present in the MLB Life Science Museum, the main repository of Tipton's Utah collections. In addition to the type specimens from Oregon (Egoscue 1968), the only other published record of *S. hubbardi* is that of Lewis et al. (1988), also from Oregon. It is unlikely that the species has been collected in Utah.

Megarthroglossus becki
Tipton & Allred 1951

Salt Lake Co.: Wasatch Mts., mouth of Little Cottonwood Canyon, 1676 m (scrub oak), 3 December 1989; 1♂, 1♀ ex *Neotoma cinerea* nest.

The species has been collected only in Utah (Kane, Piute, Utah, and Wayne counties; Tipton et al. 1979) and Arizona (Augustson and Durham 1961). This is the northernmost record known, some 37 km north of the type locality in the Wasatch Mountains. *Megarthroglossus becki* is a nest flea of woodrats, principally the bushy-tailed woodrat *Neotoma cinerea.*

Megabothris asio megacolpus
(Jordan 1929)

Rich Co.: Laketown, 22 August 1952; 11♂♂, 26♀♀ (BYU #5097-5099, 5101-5103, 5105-5119, 5121-5131, 5135, 5137, 5138, 5737, 5738) ex *Microtus montanus* nests [3 examined], coll. D E. Beck & L. Beck. Laketown, 26 June 1953; 1♂, 4♀♀ (BYU #7823-7827) ex *Microtus* nests [3 examined], coll. Beck et al. Sevier Co.: Fish Lake [south end], 5 August 1952, 1♀ (BYU #5622) ex *Microtus* sp., coll. Coffey & Killpack. Monroe Mt., 7 mi. [≈ 11 km] W of Koosharem, 30 July 1958; 1♂, 2♀♀ ex *Microtus* sp. [3 examined], coll. unknown.

The range of this boreal vole flea extends deep into south central Utah. Only two specimens are known from Idaho, including one from Bear Lake County adjacent to Rich County (Baird and Saunders 1992). Collections from Ravalli and Beaverhead counties, MT, are documented (Holland 1950), and specimens from Ravalli County are present in the Natural History Museum, London (T. M. Howard personal communication). A point-mapped record roughly on the Utah-Wyoming border given in Haddow et al. (1983) is evidently meant to be Laketown because four specimens with the same collection data as the 22 August 1952 series are present in the Natural History Museum, London (Howard personal communication).

Chaetopsylla stewarti Johnson 1955

Utah Co.: Wasatch Mts., "near summit of Alpine Loop" [American Fork or Provo Canyons], 24 November 1965; 6♂♂, 6♀♀ ex *Mustela frenata*, coll. D. Andrews. Summit Co.: Uinta Mts., 1/2 mi. [0.8 km] E Bald Mt., 8 August 1957, 1♂ ex *Martes* sp., coll. D. Allred & M. Killpack.

These specimens are the only ones known, other than the type series (from Cache County, Lewis and Lewis 1994). Weasels seem to be the preferred host.

Euhoplopsyllus glacialis lynx
(Baker 1904)

Salt Lake Co.: Wasatch Mts., Big Cottonwood Canyon, vic. Redman Campground, 2560 m, 17 August 1988; 3♀♀, 1♂ ex *Lepus americanus* (UU #28674). Big Cottonwood Canyon, 2280 m, 30 August 1988, 1♀ ex *Lepus americanus.* Big Cottonwood Canyon, vic. Butler

Fork trailhead, 2182 m, 19 May 1991, 2♂♂ ex *Lepus americanus*.

Previously unknown in Utah, the nearest published records are for Ravalli County, MT (Kohls 1940), more than 570 km to the north. The type locality is Moscow, ID, about 790 km to the northwest (Baker 1904). This flea is consistently found on the snowshoe hare (*Lepus americanus*) and its predator, the lynx (*Lynx canadensis*). The form *E. glacialis affinis* is common in Utah and surrounding states on rabbits and jackrabbits (*Sylvilagus* spp. and *Lepus* spp. other than *L. americanus*). Questionable records of *E. g. lynx* from the states of Tamaulipas and Veracruz, Mexico (ex *Sylvilagus floridanus* and unidentified *Sylvilagus* sp.), are listed by Ayala et al. (1988).

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GREAT BASIN NATURALIST Vol. 55, No. 1, January 1995

CONTENTS

Articles

Life histories of stoneflies (Plecoptera) in the Rio Conejos of southern Colorado .... R. Edward DeWalt and Kenneth W. Stewart 1

Pollinator sharing by three sympatric milkvetches, including the endangered species *Astragalus montii* .... S. M. Geer, V. J. Tepedino, T. L. Griswold, and W. R. Bowlin 19

Factors affecting selection of winter food and roosting resources by porcupines in Utah .... Dave Stricklan, Jerran T. Flinders, and Rex G. Cates 29

Historic expansion of *Juniperus occidentalis* (western juniper) in southeastern Oregon .... Richard F. Miller and Jeffery A. Rose 37

Rangeland alpha diversities: Harvey Valley, Lassen National Forest, California ... . Raymond D. Ratliff 46

Effects of salinity on establishment of *Populus fremontii* (cottonwood) and *Tamarix ramosissima* (saltcedar) in southwestern United States .... Patrick B. Shafroth, Jonathan M. Friedman, and Lee S. Ischinger 58

Names and types of *Hedysarum* L. (Fabaceae) in North America .... Stanley L. Welsh 66

Whipworm (*Trichuris dipodomys*) infection in kangaroo rats (*Dipodomys* spp.): effects on digestive efficiency .... James C. Munger and Todd A. Slichter 74

Local distribution and foraging behavior of the spotted bat (*Euderma maculatum*) in northwestern Colorado and adjacent Utah .... Jay F. Storz 78

The *Chrysothamnus-Ericameria* connection (Asteraceae) ..... Loran C. Anderson 84

Notes

Reproductive behavior in Merriam's chipmunk (*Tamias merriami*) .... Stephen B. Compton and J. R. Callahan 89

Additional records of fleas (Siphonaptera) from Utah .... James R. Kucera 92

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DIETS OF YOUNG COLORADO SQUAWFISH AND OTHER SMALL FISH IN BACKWATERS OF THE GREEN RIVER, COLORADO AND UTAH

Robert T. Muth[1] and Darrel E. Snyder[1]

ABSTRACT.—We compared diet of young-of-year Colorado squawfish (*Ptychocheilus lucius*), an endangered cyprinid, with diets of other fish <75 mm total length (TL) collected from backwaters of the Green River between river kilometers 555 and 35 during summer and autumn 1987. Species included native *Rhinichthys osculus*, *Catostomus discobolus*, and *C. latipinnis*, and nonnative *Cyprinella lutrensis*, *Notropis stramineus*, *Pimephales promelas*, *Ictalurus punctatus*, and *Lepomis cyanellus*. For each species, diet varied with size and between upper and lower river reaches but not between seasons for fish of similar size. Larval chironomids and ceratopogonids were principal foods of most fishes. Copepods and cladocerans were important in diets of *P. lucius* <21 mm TL and *L. cyanellus* <31 mm TL. *Catostomus discobolus* was the only species that ate moderate amounts of algae. Fish (all larvae) were in digestive tracts of only 10 *P. lucius* (21–73 mm TL), about 1% of *P. lucius* analyzed. High diet overlap occurred between some size-reach groups of *P. lucius* and *C. lutrensis*, *R. osculus*, *C. latipinnis*, *I. punctatus*, and *L. cyanellus*. Potential for food competition between young-of-year *P. lucius* and other fishes in backwaters appeared greatest with the very abundant *C. lutrensis*.

Key words: Ptychocheilus lucius, Cyprinella lutrensis, *nonnative fishes, young-of-year, diets, diet overlap, backwaters, Green River.*

Wild populations of federally endangered Colorado squawfish (*Ptychocheilus lucius*) persist only in the upper Colorado River basin. They are most abundant in the Green and Yampa rivers of eastern Utah and northwestern Colorado (Tyus 1991a). Decline of this and other native fishes in the Colorado River basin has been attributed to habitat alterations caused by water development and introduction and proliferation of nonnative fishes (Carlson and Muth 1989, Minckley 1991).

Backwaters of the Green River below its confluence with the Yampa River are important nursery areas for young-of-year (YOY) Colorado squawfish (Nesler et al. 1988, Haines and Tyus 1990, Tyus and Haines 1991). Ichthyofauna of these backwaters is dominated by nonnative fishes, especially red shiner (*Cyprinella lutrensis*; Tyus et al. 1982, Haines and Tyus 1990). This observation has led to a hypothesis that nonnative fishes adversely affect survival of young Colorado squawfish through competition or predation. Stanford (1993) suggested that strong food-web interactions between native and nonnative fishes probably occur, but dietary relationships have not been adequately documented (Haines and Tyus 1990, Ruppert et al. 1993). Our objectives were to (1) describe diets of YOY Colorado squawfish and other small fish in backwaters of the Green River and (2) examine diet overlap and potential for competition with Colorado squawfish.

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METHODS

Samples of small fish were provided by the U.S. Fish and Wildlife Service Field Station at Vernal, UT. These were collected from backwaters of the Green River during summer (30 June–27 August) and autumn (22 September–10 December) 1987. The study area extends from confluence of the Green and Yampa rivers in Echo Park, Dinosaur National Monument, CO, to Turks Head in Canyonlands National Park, UT—river kilometer (RK) 555 to 35 above confluence with the Colorado River. Upper and lower reaches are divided at Sand Wash (RK 346), UT, a convenient access point just above Desolation Canyon. Each river reach began with a rocky, high-gradient (1.3–2.1 m/km) segment and continued with a sand- and silt-laden, low-gradient (0.2–0.4 m/km) segment known for relatively high catches of YOY Colorado squawfish (Haines and Tyus 1990, Tyus and Haines 1991). The river was further divided into 8-km sections starting from a random location within each reach to help assure an even distribution of collection sites.

Backwaters were defined as shallow (typically <0.5 m maximum depth), ephemeral embayments with negligible water velocity. Substrates consisted of silt and sand or silt and mud, sometimes overlaying or interspersed with gravel or cobble. Backwaters had little or no rooted aquatic vegetation, but some had dense mats of algae. Two backwaters were sampled weekly in each 8-km section during daylight (1000–1800 h) using 1-m^2 seines (0.8-mm^2 mesh) in summer and 1-m × 3-m seines (3.2-mm × 4.8-mm mesh) in autumn. Fish were killed and fixed in 10% formalin immediately after collection.

Up to five specimens ≤ 20 mm total length (TL) and five >20 mm TL of each fish species, representing graded size series, were selected from each sample. Each digestive tract (from esophagus to vent) was removed, opened, and visually assessed for percent fullness. Food items were identified to lowest practical taxon, and a visual estimate was made of percentage contributed by each taxon to total volume of food in each digestive tract (Larimore 1957, Mathur 1977). For diet analyses, food-item taxa (total of 124) were grouped into 20 family, order, or broader-based categories, sometimes divided according to habitat (e.g., aquatic or terrestrial).

Data for each fish species were stratified according to length (10-mm TL or larger intervals) by season (summer or autumn) within river reach (upper or lower). Only subsets with at least six fish containing food were included in analyses. Diet measures calculated for each subset were (1) mean percentage each food category contributed to total volume of food in each digestive tract (mean of volume percentages) and (2) percentage of all digestive tracts in which each food category occurred (percentage of occurrence). Wallace (1981) evaluated several diet measures and concluded that mean of volume percentages is the best measure for calculating overlap. However, percentage of occurrence is useful for describing general variations in diet (Wallace 1981, Bowen 1983).

Similarities in diet by subset between Colorado squawfish and other fishes were evaluated by Schoener's (1970) resource-overlap index:

$$\propto = 1 - 0.5\left(\sum_{i=1}^{n} |Pxi - Pyi|\right),$$

where n is the number of food categories, Pxi is the proportion of food category i (expressed as mean of volume percentages) in the diet of species x (Colorado squawfish), and Pyi is the proportion of food category i in the diet of species y (other fishes). Values range from 0.0 (no overlap) to 1.0 (complete overlap). When data on resource availability are absent, Schoener's index is one of the best indices available for calculating resource overlap (Hurlbert 1978, Linton et al. 1981, Wallace 1981). Diet overlap is useful in helping to elucidate food relationships among species and has been considered "biologically important" when values exceed 0.60 (Zaret and Rand 1971, Matthews and Hill 1980, Galat and Vucinich 1983).

RESULTS

Digestive tracts from 2554 fish representing 15 species were examined for food items;

<3% were empty, mostly from fish ≤ 13 mm TL. After subsets with <6 specimens containing food were eliminated from the data set, 2297 specimens representing nine species remained for diet analyses. Native fish included 972 Colorado squawfish (7.5–73.0 mm TL, mean = 19.1), 35 speckled dace (*Rhinichthys osculus*; 23.1–39.8 mm TL, mean = 28.1), 42 bluehead sucker (*Catostomus discobolus*; 23.0–58.9 mm TL, mean = 35.9), and 21 flannelmouth sucker (*C. latipinnis*; 32.0–64.3 mm TL, mean = 47.9). Nonnative fish included 729 red shiner (11.3–74.5 mm TL, mean = 29.1), 92 sand shiner (*Notropis stramineus*; 22.2–53.2 mm TL, mean = 31.0), 330 fathead minnow (*Pimephales promelas*; 11.0–65.9 mm TL, mean = 32.5), 58 channel catfish (*Ictalurus punctatus*; 22.5–70.0 mm TL, mean = 42.9), and 18 green sunfish (*Lepomis cyanellus*; 20.7–56.8 mm TL, mean = 39.6).

Characterization of Diets

No major or consistent seasonal differences in diet measures were observed within species for fish of similar size. Accordingly, summer and autumn data were combined for species and lengths by river reach. Trends in values of proportional importance of each food category were similar between the two diet measures for all fishes; therefore, only means of volume percentages are reported.

Diets consisted mostly of insects, zooplankton, algae, seeds, and organic and inorganic debris; but relative importance of these food categories varied among fishes or subsets within species (Table 1). Based on total number of food categories included in the diet of each fish species, diets of Colorado squawfish and red shiner were the most varied (18 and 17 food categories, respectively), followed by speckled dace (15), fathead minnow, channel catfish, and green sunfish (12 each), sand shiner (11), flannelmouth sucker (9), and bluehead sucker (6). Variety of food consumed was greater in the lower than upper reach for red shiner, Colorado squawfish, flannelmouth sucker, channel catfish, and green sunfish, whereas diets of sand shiner, fathead minnow, and speckled dace were more varied in the upper reach (diet of bluehead sucker was analyzed for fish from the upper reach only). Diet variety relative to fish length was greatest in red shiner, sand shiner, fathead minnow, Colorado squawfish, speckled dace, and bluehead sucker 21–30 or 31–40 mm TL and in flannelmouth sucker, channel catfish, and green sunfish >40 mm TL. Mean percent fullness of digestive tracts was highest in fish 21–30 or 31–40 mm TL for all species.

Aquatic insects were a principal part of diets for all fishes except fathead minnow and bluehead sucker. Of identifiable insects, immature dipterans (especially larval chironomids) were predominant in digestive tracts. Larval chironomids were represented by at least 21 genera, the most common being *Chironomus* followed by *Rheotanytarsus, Eukiefferiella, Polypedilum, Tanytarsus, Cricotopus,* and *Micropsectra.* Representative families of other immature dipterans were (in order of importance) Ceratopogonidae, Simuliidae, Dolichopodidae, Empididae, Muscidae, and Tipulidae. Proportional contribution of immature dipterans to diets of red shiner, sand shiner, speckled dace, and flannelmouth sucker was higher in the lower than upper reach. Relative importance of immature dipterans in diets of red shiner, sand shiner, and speckled dace decreased and utilization of other insects increased as fish length increased. Conversely, relative importance of immature dipterans in diets of Colorado squawfish and channel catfish increased or remained high with increasing fish length. Corixids, larval and adult aquatic coleopterans (predominantly Dytiscidae, Elmidae, Haliplidae, and Hydrophilidae), trichopteran larvae (mainly Hydropsychidae and Hydroptilidae), and ephemeropteran nymphs (predominantly Baetidae and Heptageniidae) were minor components of diets for all fishes (<10% of food volume) except larger red shiner, speckled dace, and green sunfish.

Red shiner and sand shiner ate more semiaquatic or terrestrial insects than other fishes. Semiaquatic insects consumed were primarily larval and adult coleopterans (predominantly Heterocercidae and Staphylinidae) and adult hymenopterans (Scelionidae). Terrestrial insects consumed were primarily hemipterans and formicids.

All fishes ate zooplankton, but it was particularly important in diets of Colorado squawfish <31 mm TL (especially <21 mm TL), green sunfish <31 mm TL, and, to a lesser extent, red shiner and channel catfish <31 mm TL and flannelmouth sucker. Cladocerans (many identified as *Daphnia, Eurycercus,* and *Macrothrix*) and especially cyclopoid copepods

TABLE 1. Diets by total-length intervals (mm) of nine fish species collected during summer and autumn 1987 from sure is mean percentage contributed by each food category to total volume of food in each digestive tract (mean of vol-

	Red shiner				Sand shiner			Fathead minnow				Colorado squawfish	
Food category	11–20	21–30	31–40	>40	21–30	31–40	>40	11–20	21–30	31–40	>40	<11	11–20
Upper reach[a]													
Insects													
Unidentifiable parts	11	9	25	37	3	9	22		2	1			1
Semiaquatic or terrestrial	1	4	6		12	5				<1			
Diptera immatures	30	27	29	13	25	19	3		7	4	4	13	70
Chironomidae adults	1	3	3	10	9	4	9						
Anisoptera nymphs													
Aquatic Coleoptera		3	10										
Corixidae		<1	1	10									
Trichoptera larvae	1	1	1									1	
Ephemeroptera nymphs		1					2						
Zooplankton													
Cladocera and Copepoda	7	6	3	3					<1	<1		26	16
Rotifera	6	<1							<1	<1	<1	16	1
Ostracoda						1			1				
Gammaridae													<1
Hydracarina												2	<1
Invertebrate eggs		1	1		<1	1				<1	<1	3	1
Nematoda	<1				1							6	1
Fish													
Plant seeds	7	9	<1	<1					1	1	4		<1
Algae	2	4	1		1	2			2	2	2	2	
Organic-inorganic debris	35	32	22	26	50	60	64		87	93	90	31	10
Number of fish	45	140	63	17	40	19	7	0	108	75	26	40	305
Mean % fullness of digestive tracts	52	64	44	38	81	77	73		83	84	75	40	59
Lower reach[a]													
Insects													
Unidentifiable parts	3	13	16	23	12	14	6		2	2	1		
Semiaquatic or terrestrial	9	8	10	11		2							<1
Diptera immatures	55	36	32	28	37	31	27	9	9	4	<1	19	47
Chironomidae adults	1	3	5	2									
Aquatic Coleoptera		2	1	3			6						
Corixidae			<1										
Trichoptera larvae		1	1	1								6	<1
Ephemeroptera nymphs	<1	1											
Anisoptera nymphs													
Zooplankton													
Cladocera and Copepoda	6	5	3	<1				1	1	<1	<1	29	35
Rotifera		<1	<1							<1		7	3
Ostracoda		<1	<1	<1			2		<1				
Gammaridae													
Hydracarina													
Invertebrate eggs	<1	1	<1			3						5	2
Nematoda		1	<1		9	18		1				1	1
Fish													
Plant seeds	9	7	4	5					<1		2		
Algae	1	1	1	1	2	<1		1	1	2	3		<1
Organic-inorganic debris	18	23	26	28	40	32	59	88	87	93	95	33	10
Number of fish	62	208	138	56	10	10	6	9	31	49	32	27	301
Mean % fullness of digestive tracts	58	60	49	36	66	52	37	72	85	80	78	45	70

[a]Upper reach = confluence of Green and Yampa rivers at RK 555 (river kilometers above confluence of the Green and Colorado rivers) in Echo Park, Dinosaur National Monument, CO, to Sand Wash, UT (RK 346); lower reach = Sand Wash to Turks Head, Canyonlands National Park, UT (RK 35).

backwaters in two reaches of the Green River below its confluence with the Yampa River, Colorado and Utah. Diet mea-ume percentages).

Colorado squawfish			Speckled dace		Bluehead sucker			Flannelmouth sucker		Channel catfish			Green sunfish	
21–30	31–40	>40	21–30	31–40	21–30	31–40	>40	31–40	>40	21–30	31–40	>40	21–30	>40
Upper reach[a]														
10			34									4		
			2									1		
72	52	54	31		5	1		28	22			70		66
			8											
		8												13
	2		3											12
			4											2
		<1						8	13					1
1					1	<1								
									14					
2	6		5		<1	1								
	6											10		
	25	29												
			8		2	<1		<1						
					11	11	10		<1					
13	10	10	3		82	88	90	64	52			14		6
46	12	11	18	0	14	19	9	8	6	0	0	8	0	6
61	50	57	73		88	78	81	77	63			78		71
Lower reach[a]														
1	1		9	8						8	2	13		10
1	1									6	1	3		5
61	66	78	65	49					52	55	83	68	48	19
1	4											5	1	
<1				11								1		
														12
2	2		7	15								1		
				3										34
18	13	1	3						7	13	2		44	2
<1									<1					
									3					14
				5										
<1														
4														
1	2	6							<1	3		<1	<1	
<1	2	5												
1			8							3				
<1			<1						4	<1				
10	10	10	7	8					34	13	13	11	8	4
174	37	19	11	6	0	0	0	0	7	8	16	26	6	6
80	54	59	79	71					75	88	73	71	77	59

(many identified as *Cyclops*) represented most zooplankton found in digestive tracts. Identified genera of rotifers included *Brachionus*, *Cephalodella*, *Keratella*, *Lecane*, *Monostyla*, *Polyarthra*, and *Trichocerca*. Proportion of zooplankton in diets of all fishes tended to decrease with increasing fish length.

Bluehead sucker was the only species that ate moderate amounts of algae (10–30% of food volume); other fishes consumed minor amounts. Algae consisted mostly of six diatom genera (*Cymbella*, *Fragilaria*, *Gyrosigma*, *Navicula*, *Surirella*, and *Synedra*), one desmid genus (*Closterium*), and, to a lesser extent, *Pediastrum* (a colonial green alga). Most digestive tracts contained debris that accounted for moderate or large proportions of gut contents (>30%) in all fishes except speckled dace and green sunfish. It was over 80% of gut content in fathead minnow and bluehead sucker. Debris consisted of fibrous particles of vascular plant tissue usually mixed with large amounts of clay particles and sand grains, suggesting bottom feeding. Seeds (many identified as tamarisk [*Tamarix gallica*]) were eaten by all fishes, especially red shiner <31 mm TL.

Two observations were unique to Colorado squawfish. Fish larvae were found in digestive tracts of 10 Colorado squawfish (about 1% of total examined); 1 was 21 mm TL, 8 were 36–48 mm TL, and 1 was 73 mm TL (probably a yearling). No fish were detected in digestive tracts of other species. Of the 18 fish larvae found, most were too digested for species identification or accurate length measurement, but all were cypriniforms (mostly cyprinids) and probably ≤ 10 mm TL. Six fish larvae (6–9 mm TL) were identified as red shiner, and one (about 8 mm TL) as fathead minnow. Interestingly, the smallest Colorado squawfish had four prey fish (all red shiner), whereas only one or two fish were found in digestive tracts of the others. Gut contents of six Colorado squawfish, 36–48 mm TL, and the 73-mm-TL specimen were exclusively fish; those for the remaining specimens were 70–80% fish. Digestive tracts of six Colorado squawfish contained 2–6 cestode parasites (probably *Proteocephalus ptychocheilus*; Flagg 1982); cestodes were not found in guts of other fishes. Colorado squawfish infested with cestodes were larger than 27 mm TL and were collected from both river reaches in autumn.

Diet Overlap

Degree of diet overlap between YOY Colorado squawfish and other fishes was influenced mainly by zooplankton and especially immature dipterans (Table 2). Within each reach, diet overlap for all length intervals of Colorado squawfish generally decreased as lengths of other species increased. Degree of diet overlap among fish of similar size was generally greater in the lower than upper reach. Overlap values were <0.60 (range = 0.10–0.59) for most comparisons; generally, values were lowest for comparisons with fathead minnow and bluehead sucker (range = 0.10–0.44). Biologically important overlap (values >0.60) occurred only between Colorado squawfish >10 mm TL and some size-reach groups of native speckled dace and flannelmouth sucker and nonnative red shiner, green sunfish, and especially channel catfish. These higher overlap values were primarily attributed to high proportions of larval chironomids in diets and, secondarily, especially for diet overlap with green sunfish >40 mm TL (upper reach) and 21–30 mm TL (lower reach), to proportions of zooplankton. Degree of diet overlap was greatest with channel catfish and green sunfish.

DISCUSSION

Comparisons among food-habits investigations are difficult because of differences in study design, location, and season. However, our observations on diets of native and nonnative fishes in backwaters of the Green River generally agree with results of prior studies in the upper Colorado River basin (e.g., Vanicek and Kramer 1969, Jacobi and Jacobi 1982, McAda and Tyus 1984) and reported food habits of the nonnative species within their native ranges (e.g., Carlander 1969, 1977, Pflieger 1975, Harlan et al. 1987). Larger YOY or yearling red shiner, sand shiner, speckled dace, flannelmouth sucker, channel catfish, and green sunfish eat mainly immature aquatic insects. Diets of larger YOY or yearling fathead minnow and bluehead sucker consist mostly of algae and organic debris. Diet of YOY Colorado squawfish consists primarily of zooplankton and immature insects (especially chironomid larvae) and occasionally includes fish.

Reported size at which wild Colorado squawfish shift to a more piscivorous diet varies, but generally fish become an important food item after Colorado squawfish attain a length of >40 mm. Osmundson and Kaeding (1989) suggested that slower growth and poorer condition of YOY and especially yearling Colorado squawfish in grow-out ponds with lower densities of appropriate-size forage fish might have been caused by higher reliance on insect forage. Identifiable fish reported in digestive tracts of YOY Colorado squawfish here and by McAda and Tyus (1984) and Grabowski and Hiebert (1989) were either red shiner or fathead minnow larvae. These nonnative species are short-lived fractional spawners (Gale and Buynak 1982, Gale 1986) and are typically present in high numbers and at appropriate forage sizes in backwaters of the Green River throughout summer and autumn (Tyus et al. 1982, Karp and Tyus 1990). Karp and Tyus (1990) suggested that although the abundance of small nonnative prey fishes in the Green River might benefit growth of young Colorado squawfish, the benefit might be countered by the aggressive nature of some nonnative fishes, which could have negative effects on growth and survival of young Colorado squawfish. In their laboratory experiments on behavioral interactions, Karp and Tyus observed that red shiner, fathead minnow, and green sunfish shared activity schedules and space with Colorado squawfish and exhibited antagonistic behaviors toward smaller Colorado squawfish.

We could not effectively evaluate competition for food between YOY Colorado squawfish and other fishes because study design did not provide for estimation of resource abundance and availability, intraspecific diet selectivity, and effects of interspecific use of important resources. Direct evidence for interspecific competition should be determined through experiments demonstrating that shared use of a limited resource negatively affects one or more of the species (Schoener 1983, Underwood 1986, Wiens 1992). Additionally, we assume gut contents represented food consumed in the backwaters of capture, but this might not always have been the case. Tyus (1991b) observed that although young Colorado squawfish in the Green River were found mostly in backwaters, some moved to or from other habitats during 24-h periods. We found that diet overlap for most comparisons with Colorado squawfish was below the level generally considered biologically important (Table 2). Although not conclusive, these comparisons suggest either general resource partitioning or differences in diet preferences. Diet overlap values were considered biologically important only for comparisons with certain size-interval, river-reach groups of five fishes.

Because interspecific demand for resources might not exceed supply, Bowen (1983) noted that even extensive diet overlap is not conclusive evidence for competition. Accordingly, McAda and Tyus (1984), who also used Schoener's index to examine diet overlap between YOY Colorado squawfish and nonnative fishes in the Green River, suggested that high diet overlap they observed between Colorado squawfish 22–40 mm TL and channel catfish 19–55 mm TL (overlap value = 0.60) and especially red shiner 15–69 mm TL (overlap values 0.70–0.80) might reflect shared use of abundant resources, primarily immature dipterans, rather than competition. The same may be true for higher diet overlaps we observed. Ward et al. (1986) reported that chironomids, the principal food category resulting in high diet overlap, were among the more common benthic invertebrates in the Colorado River basin.

We observed that overlap values were generally higher and, for most fishes, diet variety was greater in the lower than upper reach, perhaps because food resources were more abundant and diverse in backwaters of the lower reach. Based on observations during summer and autumn 1979–1988, Haines and Tyus (1990) found that backwaters in the upper and lower reaches were similar in mean surface area, but that those in the lower reach were shallower and warmer, conditions that may favor higher productivity. Also, within the upper reach, Grabowski and Hiebert (1989) noted that during summer and autumn 1987–88 concentrations of backwater nutrients, particulate organic matter, phytoplankton, zooplankton, and benthic macroinvertebrates (particularly chironomid larvae) increased progressively downstream. They suggested this trend was due to attenuation of flow releases from Flaming Gorge Reservoir (located near the Wyoming-Utah border) at downstream sites that reduced the degree of water exchange between the main channel and backwaters and allowed for greater backwater warming and stability.

TABLE 2. Diet overlap by total-length (TL) intervals (mm) between young-of-year Colorado squawfish and eight other confluence with the Yampa River, Colorado and Utah. Overlap values were calculated using Schoener's (1970) index asterisk (*).

TL of Colorado squawfish	Red shiner								Sand shiner						Fathead minnow		
	Upper reach[a]				Lower reach[a]				Upper			Lower			Upper		
	11–20	21–30	31–40	>40	11–20	21–30	31–40	>40	21–30	31–40	>40	21–30	31–40	>40	21–30	31–40	>40
<11	0.59	0.54	0.40	0.43	0.42	0.49	0.50	0.47	0.46	0.47	0.35	0.53	0.55	0.52	0.40	0.37	0.38
11–20	0.49	0.45	0.43	0.31	0.63*	0.53	0.47	0.38	0.37	0.31	0.14	0.49	0.45	0.38	0.18	0.15	0.15
21–30	0.55	0.51	0.53	0.41	0.74*	0.57	0.51	0.42	0.42	0.43	0.27	0.49	0.47	0.38	0.23	0.19	0.23
31–40	0.40	0.39	0.40	0.27	0.73*	0.57	0.52	0.42	0.35	0.29	0.12	0.50	0.45	0.38	0.17	0.13	0.15
>40	0.39	0.37	0.39	0.35	0.65*	0.47	0.44	0.37	0.34	0.28	0.12	0.53	0.47	0.37	0.17	0.13	0.14

[a]Upper reach = confluence of Green and Yampa rivers at RK 555 (river kilometers above confluence of Green and Colorado rivers) in Echo Park, Dinosaur National Monument, CO, to Sand Wash, UT (RK 346); lower reach = Sand Wash to Turks Head, Canyonlands National Park, UT (RK 35)

Alternatively, greater diet overlap and variety in the lower reach might have been a reflection of a difference in backwater availability between the upper and lower reaches. Tyus and Haines (1991) reported about 150% more backwaters per kilometer in the upper than lower reach. Fishes in the lower reach might have been more crowded in available backwaters, resulting in greater shared use and broader intraspecific use of available food.

McAda and Tyus (1984) attributed reductions in diet overlap between Colorado squawfish >40 mm TL and red shiner or channel catfish to decreased consumption of immature dipterans and increased consumption of fish by Colorado squawfish. However, Ruppert et al. (1993) reported fish larvae in digestive tracts of 15% of adult red shiner (36–79 mm TL) from ephemeral shoreline embayments near confluence of the Green and Yampa rivers. Unlike our study, they sampled on a diel basis and killed fish with an overdose of anesthetic before preservation to minimize possible regurgitation. Their results suggest that high diet overlap between young Colorado squawfish ≥ 40 mm TL and red shiner might reoccur or continue with larger, piscivorous red shiner. Although we documented high diet overlap between young Colorado squawfish >10 mm TL and other fishes in backwaters of the Green River, especially channel catfish (Table 2), only red shiner, because of its extreme abundance (Haines and Tyus 1990), is likely to be a serious competitor for food with young Colorado squawfish. Red shiner has often been implicated in decline of native fishes of the American Southwest (e.g., Minckley 1973, Greger and Deacon 1988, Rinne 1991).

Competition might also be a factor between smaller specimens of both Colorado squawfish and other fishes. Few specimens <21 mm TL, other than red shiner and fathead minnow 11–20 mm TL, were available for comparisons with Colorado squawfish. However, as for smaller Colorado squawfish, zooplankton would likely be an important component of their diets (Joseph et al. 1977), and corresponding overlap values would be high, especially for specimens <11 mm TL. Although dense populations may develop in backwaters, zooplankton may be limited under certain conditions because plankton communities in rivers are subject to dramatic spatial or temporal fluctuations in abundance and diversity (Hynes 1970, Welcomme 1985, Ward 1989). In support of this generalization, Grabowski and Hiebert (1989) reported that zooplankton densities were higher in backwaters than in main-channel habitats within the upper reach and documented both spatial and temporal fluctuations in zooplankton abundance. They also observed higher concentrations of zooplankton in more confined backwaters than those with a broad connection to the river and suggested that densities were influenced by extent of water exchange between backwaters and the main river.

In conclusion, we found high diet overlap between YOY Colorado squawfish and several small size groups of other fish species in Green River backwaters. Because of the extreme abundance of red shiner, we speculate that diet overlap could result in food competition

fish species collected during summer and autumn 1987 from backwaters in two reaches of the Green River below its
with mean of volume percentages as the diet measure; values >0.60 (biologically important overlap) are marked with an

Fathead minnow				Speckled dace			Bluehead sucker			Flannelmouth sucker			Channel catfish				Green sunfish		
Lower				Upper	Lower		Upper			Upper		Lower	Upper	Lower			Upper	Lower	
11–20	21–30	31–40	>40	21–30	21–30	31–40	21–30	31–40	>40	31–40	>40	>40	>40	21–30	31–40	>40	>40	21–30	>40
0.44	0.43	0.37	0.33	0.21	0.36	0.34	0.39	0.35	0.34	0.52	0.57	0.59	0.34	0.46	0.34	0.30	0.21	0.56	0.25
0.22	0.21	0.15	0.11	0.37	0.59	0.57	0.16	0.12	0.11	0.46	0.45	0.65*	0.83*	0.72*	0.61*	0.57	0.73*	0.91*	0.26
0.21	0.21	0.15	0.12	0.52	0.76*	0.61*	0.20	0.16	0.19	0.42	0.36	0.69*	0.89*	0.81*	0.75*	0.75*	0.73*	0.75*	0.27
0.21	0.21	0.14	0.10	0.42	0.78*	0.61*	0.14	0.11	0.11	0.38	0.31	0.69*	0.68*	0.81*	0.79*	0.82*	0.61*	0.69*	0.27
0.21	0.20	0.14	0.10	0.35	0.74*	0.58	0.14	0.10	0.10	0.38	0.31	0.63*	0.64*	0.69*	0.89*	0.77*	0.68*	0.57	0.24

and might have a negative impact on Colorado squawfish growth, condition, or survival. Studies are needed to better assess the type and strength of interactions between native and nonnative fishes in backwater food webs under present regulated flow regimes and to define factors affecting these interactions.

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INVERTEBRATE FAUNA OF WASTEWATER PONDS IN SOUTHEASTERN IDAHO

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ABSTRACT.—Water column invertebrates were sampled with 3.8-L activity traps in 15 sewage, industrial, and radioactive wastewater ponds at the Idaho National Engineering Laboratory in southeastern Idaho. One collection was made per pond, per month, during all months the ponds were ice-free from June 1990 through July 1991. In addition, nutrient and selected heavy metal concentrations in pond water were determined in July 1991. Arsenic, barium, boron, lead, selenium, and mercury were detected in ponds. Sewage ponds generally had higher nitrogen and phosphorus levels than industrial and radioactive ponds. Of the 30 aquatic invertebrate taxa collected, the most ubiquitous were Rotifera, Daphnidae, Eucopepoda, Ostracoda, Acari, Baetidae, Corixidae, Notonectidae, Dytiscidae, and Chironomidae. Activity trap samples from sewage ponds contained more Rotifera, Daphnidae, and Notonectidae, whereas industrial ponds yielded more Chydoridae, Acari, and Baetidae. Numbers of Oligochaeta, Eucopepoda, Ostracoda, Corixidae, Dytiscidae, and Chironomidae collected were not significantly different between sewage and industrial ponds. Compared with natural systems, these ponds had fewer taxa, but a greater number of individuals of most taxa. The high number of invertebrates collected is attributed to the lack of fish in wastewater ponds and the high levels of nitrogen and phosphorus, particularly in sewage ponds.

Key words: aquatic invertebrates, sanitary wastewater, industrial wastewater, Idaho National Engineering Laboratory.

Constructed ponds have been a common tool in wastewater treatment for decades (Gloyna et al. 1976). Wastewater ponds are constructed in a variety of manners and used in various treatment procedures, from settling ponds to ponds with various aquatic macrophytes that enhance removal of nutrients and break down organic materials (Brix 1993). Recently, constructed wetlands have also been incorporated into many wastewater treatment systems associated with municipalities and industry (Task Force on Natural Systems 1990, Moshiri 1993). Wastewater ponds and wetlands are also associated with federal research sites such as the Idaho National Engineering Laboratory (INEL) in southeastern Idaho and the Hanford Site in south central Washington.

Wastewater ponds at INEL receive sanitary, industrial, and radioactive waste produced at the facility. Other than wildlife watering cisterns and ephemeral rain pools, waste disposal ponds are usually the only surface water at INEL and, as such, attract wildlife (Halford and Millard 1978, Howe and Flake 1989, Millard et al. 1990, Cieminski 1993). Migrating and resident waterfowl, shorebirds, blackbirds, and swallows use the ponds heavily, feeding partially or exclusively on aquatic invertebrates, and on invertebrates that have emerged from the ponds (Millard et al. 1990, Cieminski 1993).

Most studies of macroinvertebrates, especially insects, in conjunction with waste treatment have been limited to studies of benthic invertebrate assemblages in streams receiving raw sewage or effluent from sewage treatment plants (e.g., Klotz 1977, Kownacki 1977, Duda et al. 1982, Kondratieff and Simmons 1982, Kondratieff et al. 1984, Chadwick et al. 1986, Lewis 1986, Crawford et al. 1992). Literature on plankton and nekton in constructed ponds focuses mainly on pathogens, and microscopic flora and fauna important in waste decomposition, such as bacteria, protozoa, and algae (Goulden 1976, Task Force on Natural Systems 1990).

Because the invertebrate fauna of wastewater ponds attracts wildlife, it is important to understand invertebrate communities of the ponds, as well as if and how they differ from natural communities. Our objectives were to (1) provide baseline data on invertebrate

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resources available to migrating birds in constructed waste ponds and (2) determine if nutrients and selected heavy metals in ponds influence invertebrate populations.

STUDY SITE

The 231,600-ha INEL lies in Butte, Bonneville, Bingham, Clark, and Jefferson counties, ID, on the western edge of the Snake River plain near the foothills of the Lost River, Lemhi, and Bitterroot mountain ranges (Fig. 1). Topography at INEL is flat to rolling, with elevation ranging from 1463 m to 1829 m.

Big Lost River, Little Lost River, and Birch Creek drainages terminate in playas on or near INEL; flow is intermittent and largely diverted for agriculture. During this study no surface water flowed onto INEL. Plant communities are dominated by big sagebrush (*Artemisia tridentata*), low sagebrush (*A. arbuscula*), and three-tipped sagebrush (*A. tripartita*) (McBride et al. 1978).

INEL lies in a semiarid, cold desert. Annual temperatures range from −42°C to 39°C. Average annual precipitation is 19.1 cm, 40% of which falls from April through June (Clawson et al. 1989). Precipitation levels are lowest in July. Snowfall averages 71.3 cm per year, and snow cover can persist from December through March.

Wastewater ponds on INEL contained sanitary waste (eight ponds), industrial waste (four ponds), or radioactive waste (three ponds) (Fig. 1). Because two radioactive ponds also contained industrial waste, in most analyses radioactive ponds were grouped with industrial ponds (as "industrial ponds") for comparison with sewage ponds.

Ponds were grouped around INEL facilities, which were 4–36 km apart. Generally, each facility had between one and four sewage ponds and an industrial waste pond. Sewage ponds ranged from 0.04 to 2.20 ha and were 0.6–2 m deep. Industrial waste ponds ranged from 0.20 to 2.24 ha and were 0.3–4.5 m deep. Seven of the sewage ponds and one industrial pond were lined to prevent infiltration into surrounding soil. Four ponds (all industrial and/or radioactive) supported emergent plant growth. A more thorough description of the ponds can be found in Cieminski (1993).

METHODS

Water samples were collected at ponds in July 1991 and analyzed for nutrients (nitrogen and phosphorus) and selected heavy metals (arsenic, barium, beryllium, boron, lead, selenium, and mercury) that could influence presence of invertebrates. Water pH was taken once at each pond at the same time water samples were collected. Further heavy metal and nutrient sampling was prohibitively expensive and time consuming. Water samples were analyzed at the U.S. Geological Survey's National Water Quality Laboratory at Arvada, CO. Collection and analysis methods were as per Brown et al. (1970) and Fishman and Friedman (1989). Data on heavy metals for pond ANLi (acronyms and names of pools are included in Tables 1 and 5) were taken from analyses conducted in 1988.

Benthic samples were not taken because most ponds had lined bottoms, or because sediment sampling was not permitted for other reasons. We collected water column invertebrates once each month to obtain gross estimates of invertebrate populations. Additional collections and identification were time- and cost-prohibitive, given our concurrent collection of bird and mammal count data at these ponds for a related project. Nevertheless, we felt that invertebrates influenced bird use of ponds, thus the need for estimates of invertebrate abundance.

Water column invertebrates were collected at all nonradioactive ponds in months the ponds were ice-free from June 1990 through May 1991. Because of restricted access to radioactive waste ponds, they were sampled only once during July 1991. Invertebrates were collected in 3.8-L activity traps (Ross and Murkin 1989) suspended horizontally 5.3 cm under the water surface for approximately 24 h. Modifications on the technique of Ross and Murkin (1989) were necessary since most ponds had artificial liners; therefore, jars could not be suspended from a pipe driven in the pond bottom. Instead, jars were suspended from floats and attached to a 50- to 300-cm-long piece of PVC pipe anchored on the pond's shore. The first sample was taken at the southeast corner of each pond. Subsequent monthly sample locations were chosen randomly based on a single-digit number of paces

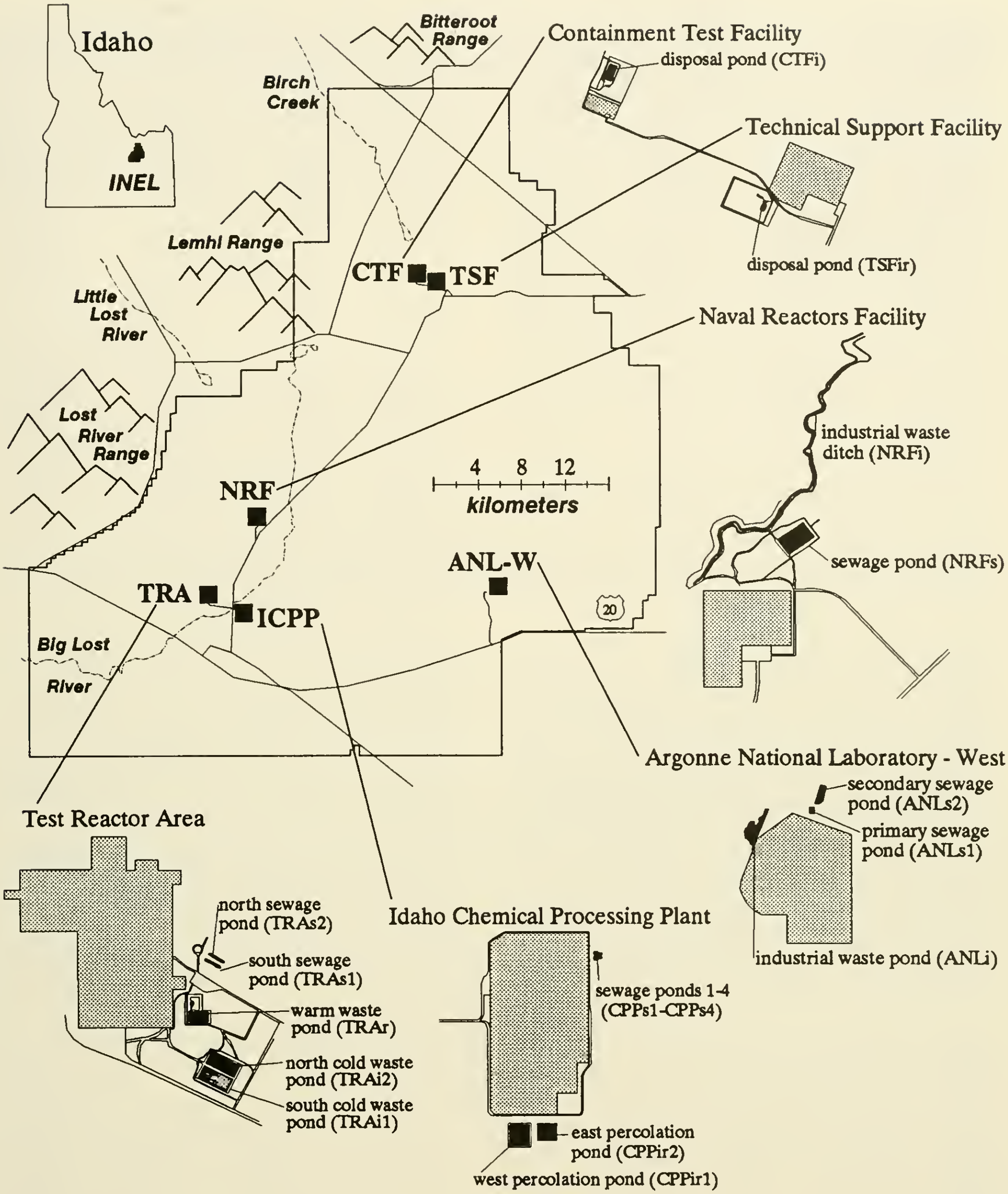
Idaho
INEL
Bitteroot Range
Birch Creek
Lemhi Range
Little Lost River
Lost River Range
Big Lost River
Containment Test Facility
disposal pond (CTFi)
Technical Support Facility
disposal pond (TSFir)
CTF
TSF
Naval Reactors Facility
industrial waste ditch (NRFi)
sewage pond (NRFs)
NRF
4 8 12
kilometers
ANL-W
20
TRA
ICPP
Argonne National Laboratory - West
secondary sewage pond (ANLs2)
primary sewage pond (ANLs1)
industrial waste pond (ANLi)
Test Reactor Area
north sewage pond (TRAs2)
south sewage pond (TRAs1)
warm waste pond (TRAr)
north cold waste pond (TRAi2)
south cold waste pond (TRAi1)
Idaho Chemical Processing Plant
sewage ponds 1-4 (CPPs1-CPPs4)
east percolation pond (CPPir2)
west percolation pond (CPPir1)

Fig. 1. Map of the Idaho National Engineering Laboratory, indicating location of facilities and wastewater ponds where invertebrate fauna was sampled. Waste type is indicated by lowercase letter in the pond code: s = sewage, i = industrial, r = radioactive.

counterclockwise from the previous sample site. Where dense emergent vegetation covered the near-shore zone, the activity trap was placed in the nearest open water.

Activity trap contents were strained through a 75-μm (No. 200) sieve and preserved in 80% propanol. In the laboratory, macroinvertebrates were removed first. Samples from shallow ponds with unlined bottoms often contained sediment. To these, rose bengal stain was added to aid in sorting microinvertebrates (Mason and Yevich 1967). Samples in which zooplankton was estimated to exceed 300 individuals were subsampled. To subsample, samples were diluted to 500 or 1000 ml and stirred while 1% of the volume was drawn out with 1- and 2-ml Henson-Stemple pipettes.

Invertebrate fauna were counted and identified to family, with the exception of the orders Oligochaeta, Acari, Araneae, Eucopepoda, Ostracoda, and Lepidoptera, and the phyla Nematoda and Rotifera. Invertebrates were identified using keys in Pennak (1989) for non-insects, Merritt and Cummins (1984) for aquatic insects, and Borror and DeLong (1971) for terrestrial insects. B. McDaniel (Plant Science Department, South Dakota State University, Brookings) identified terrestrial invertebrate families and verified other identifications.

Because data were not normally distributed, nonparametric analysis methods were used. A median test was conducted on the dozen most common invertebrate taxa to determine if their abundance in sewage ponds differed from that in industrial ponds. For each taxa, numbers of individuals collected in each sample were used in analysis. Data were pooled over all ponds, years, and months within each of the two groups: sewage ponds and industrial ponds. Pooling samples for years and ponds allowed ample sample size for comparison of gross invertebrate population differences between pond types. A median test was also run on the total number of species collected per pond during the entire sampling period to determine if species richness was greater at sewage ponds or industrial ponds. A third median test was conducted to compare invertebrate numbers between ponds with heavy metal concentrations greater than EPA criteria and those with heavy metal concentrations within EPA chronic exposure standards. Data were again pooled over all ponds, years, and months. Radioactive waste ponds were eliminated from median tests because only one sample was taken from them.

RESULTS

Water Chemistry

Heavy metal concentrations in most ponds were below criteria established by the EPA (U.S. Environmental Protection Agency 1987) (Table 1). Mercury was the only metal found in concentrations that might affect aquatic life (ponds TRAr and NRFi). However, in TRAr and NRFi mercury concentration was below the acute value of 2.4 μg/L (U.S. Environmental Protection Agency 1987).

Sewage ponds had higher nitrogen and phosphorus concentrations than industrial and radioactive ponds (Table 2). Ammonia (NH_4–N) concentrations in most ponds were within the range found in unpolluted surface water (Wetzel 1983); however, NH_4–N concentrations at ICPP sewage ponds were well above those usually found in eutrophic lakes. Nitrite (NO_2–N) concentrations indicated high organic pollution at all sewage ponds except NRFs, which was the only sewage pond where NO_2–N concentrations did not exceed those of industrial and radioactive

TABLE 1. Selected heavy metal concentrations (μg/L) in wastewater ponds at INEL, Idaho, August 1991, and EPA criteria[a].

	Pond[b]							Criteria
Metal	ANLi[c]	CPPir2	TRAr	TRAi1	NRFi	CTFi	TSFir	(μg/L)
Arsenic	9.4	2	<1[d]	<1	3	5	2	190[e]
Barium	71	<100	<100	<100	<100	<100	100	50,000
Beryllium	<5	<10	<10	<10	<10	<10	<10	5.3
Boron	—	30	50	70	120	90	10	5000
Lead	<2.1	3	3	3	2	3	2	3.2[f]
Selenium	<2	1	<1	1	2	1	1	35
Mercury	<20	<0.1	0.2	<0.1	1.4	<0.1	<0.1	0.012[g]

[a] Concentrations at or below these levels should have no adverse effects on freshwater systems. Naval Reactor Facilities officials suggested the following clarification: "The criteria in the last column have questionable applicability to the NRFi. The EPA maximum contaminant level for mercury in public community drinking water systems is 2.0 μg/L."

[b] ANLi = Argonne National Laboratory–west industrial waste pond, CPPir2 = Idaho Chemical Processing Plant east percolation pond (industrial and radioactive), TRAr = Test Reactor Area warm waste pond (radioactive), TRAi1 = Test Reactor Area south cold waste pond (industrial), NRFi = Naval Reactors Facility industrial waste ditch, CTFi = Containment Test Facility disposal pond (industrial), TSFir = Technical Support Facility disposal pond (industrial and radioactive).

[c] ANLi water sample tested at Envirodyne Engineers, St. Louis, MO, February 1988.

[d] < symbol means water sample contained less than the detection level, which follows the < symbol.

[e] Arsenic (III)

[f] At water hardness of 100 mg/L. Value is 1.3 at water hardness of 50 mg/L.

[g] Mercury (II)

TABLE 2. Nutrient concentrations in wastewater ponds at INEL, Idaho, August 1991.[a]

		Nitrogen (mg/L as N)					Phosphorus (mg/L as P)
Pond	pH[b]	NH_4^+	NO_2^-	$NO_2^- + NO_3$	NO_3	$NO_3{:}NH_4^+$	PO_4^{-3}
Sewage ponds							
ANLs2	9.02	0.19	0.17	0.46	0.29	1.50	1.20
CPPs1	7.52	11.00	2.20	4.60	2.40	0.21	4.00
CPPs2	7.23	17.00	0.69	2.40	1.71	0.10	4.80
CPPs3	7.33	17.00	0.15	0.46	0.31	0.02	6.40
CPPs4	7.43	17.00	0.14	0.43	0.29	0.02	6.10
TRAs	6.87	0.41	0.13	5.10	4.97	12.12	0.79
NRFs	9.90	0.40	0.02	0.14	0.12	0.30	3.00
Nonsewage ponds							
ANLi	7.42	0.97	0.09	0.74	0.65	0.67	1.40
CPPir2	8.80	0.04	0.05	1.30	1.25	30.49	0.01
TRAi1	7.60	0.01	0.06	1.10	1.04	104.00	0.07
TRAr	8.43	0.15	0.01	0.27	0.26	1.73	0.01
NRFi	7.42	0.01	0.01	1.60	1.59	159.00	0.40
CTFir	9.97	0.01	0.01	0.45	0.44	44.00	0.09
TSFir	9.75	0.04	0.02	0.11	0.09	2.17	0.12

[a] Samples were collected between 0800 and 1400 h, Mountain Standard Time.

[b] Water pH values fluctuate readily. According to the INEL Industrial Waste Management Information System, 1989 effluent pH ranges and numbers of months pH was sampled ( ) were as follows: ANLs1, 7.8–9.8 (7); CPPs1–4, 7.5–8.6 (12); TRAs1–2, 7.1–8.0 (10); NRFs, 7.4–11.0 (12); TRAi1–2, 7.5–8.0 (6); TRAr 6.3–6.8 (2); NRFi, 6.9–7.5 (12); TSFir, 7.1–7.9 (12).

ponds. Nitrate (NO_3–N) concentrations were not noticeably different between sewage ponds and industrial/radioactive ponds, and NO_3–N levels of all ponds were within ranges commonly found in unpolluted freshwater (Wetzel 1983).

The NO_3–N:NH_4–N ratio is an indication of organic pollution, a lower number indicating greater pollution (Wetzel 1983). The NO_3–N:NH_4–N ratio was <1 at all sewage ponds except ANLs2 and TRAs, and >1 at all industrial and radioactive ponds except ANLi. However, only in ICPP sewage ponds were ratios small enough to be considered organically contaminated (Wetzel 1983). Phosphorus concentrations at most sewage ponds were much higher than the concentration in the highest industrial/radioactive pond. Compared with maximums in uncontaminated surface waters, phosphorus concentrations in sewage ponds were 4–30 times greater, but of the industrial and radioactive ponds only concentrations in ANLi and NRFi were substantially greater (7 and 2X) (Wetzel 1983).

Invertebrate Fauna

Forty-nine taxa of invertebrates were collected from waste ponds, of which 30 were aquatic (Table 3). Most nonaquatic forms were found in small numbers. Collembola, however, were found regularly and were probably on the water surface or shaken from emergent vegetation in the collection process. In order of decreasing abundance, the main taxa collected were Rotifera, Daphnidae, Ostracoda, Eucopepoda, Chydoridae, Corixidae, Chironomidae, Oligochaeta, Baetidae, Psychodidae, Acari, Dytiscidae, and Notonectidae. The above taxa were also the most ubiquitous, except Chydoridae, Oligochaeta, and Psychodidae, which were found in large numbers but in few samples.

The number of invertebrate taxa collected per pond ranged from 5 to 22. Excluding terrestrial taxa, the number of aquatic taxa collected ranged from 4 to 16 per pond. Radioactive ponds were sampled only in July, but the number of taxa collected was almost identical to July samples from nonradioactive industrial ponds (Table 4). Statistical analyses were not performed on radioactive ponds because only one activity trap sample was collected. Industrial (ANLi, TRAi1 and 2, NRFi, and CTFi) and sewage ponds had similar (P = .11) numbers of taxa per sample.

Within most taxa, the number of individuals collected varied greatly from pond to pond (Table 5). A median test revealed that activity trap samples from sewage ponds contained more Rotifera ($P < .01$), Daphnidae ($P < .01$), and Notonectidae ($P = .04$), whereas industrial ponds yielded more Chydoridae ($P < .01$),

TABLE 3. Invertebrate taxa and mean number collected from 15 wastewater ponds at INEL, Idaho, 1990–91[a].

Taxa	$\bar{x}$/24 h (n = 96)
Phylum Rotifera	1471.14
Phylum Nematoda	0.05
Phylum Annelida	
Class Oligochaeta (aquatic earthworms)	6.32
Class Hirudinea (leeches)	
Order Rhynchobdellida	
Family Glossiphoniidae	0.02
Phylum Arthropoda	
Class Crustacea	
Order Cladocera (water fleas)	
Family Daphnidae	1351.26
Family Chydoridae	102.88
Family Sididae	0.09
Order Eucopepoda (copepods)	151.45
Order Ostracoda (seed shrimps)	317.17
Order Amphipoda (scuds)	
Family Talitridae	0.45
Class Arachnoidea	
Order Acari (mites)	1.51
Order Araneae (spiders)[b]	0.04
Class Insecta	
Order Collembola (springtails)	
Family Entomobryidae[b]	0.57
Family Onychiuridae[b]	0.30
Order Ephemeroptera (mayflies)	
Family Baetidae	5.71
Family Caenidae	0.01
Order Odonata	
Suborder Anisoptera (dragonflies)	
Family Aeshnidae	0.01
Suborder Zygoptera (damselflies)	
Family Coenagrionidae	0.31
Order Thysanoptera (thrips)[b]	
Family Thripidae (common thrips)[b]	0.11
Family Aeolothripidae (banded thrips)[b]	0.02
Order Hemiptera (true bugs)	
Family Corixidae (water boatmen)	39.76
Family Notonectidae (backswimmers)	0.53
Order Homoptera	
Family Aphidae (aphids)[b]	0.05
Family Cercopidae (spittlebugs)[b]	0.01
Family Cicadellidae (leafhoppers)[b]	0.03
Family unidentified[b]	0.25
Order Coleoptera (beetles)	
Family Chrysomelidae (leaf beetles)	0.03
Family Coccinellidae (ladybird beetles)[b]	0.01
Family Dytiscidae (predaceous diving beetles)	0.65
Family Elmidae (riffle beetles)	0.01
Family Gyrinidae (whirligig beetles)	0.01
Family Haliplidae (crawling water beetles)	0.02
Family Hydrophilidae (water scavenger beetles)	0.02
Family Ptiliidae (feather-winged beetles)	0.01
Family Staphylinidae (rove beetles)	0.02
Order Trichoptera (caddisflies)	
Family Leptoceridae	0.05
Order Lepidoptera (butterflies and moths)[b]	0.02
Order Diptera (flies)	
Family Ceratopogonidae (biting midges)	0.01
Family Psychodidae (moth flies and sand flies)	1.68
Family Chironomidae (midges)	11.52
Family Tipulidae (crane flies)	0.02
Family unidentified, adults[b]	0.80
Family unidentified, pupae	0.99
Order Hymenoptera	
Family Formicidae (ants)[b]	0.03
Family Platygasteridae[b]	0.01
Family Braconidae[b]	0.01
Family Encyrtidae[b]	0.01
Family Pteromalidae[b]	0.01
Family Scelionidae[b]	0.01
Family Sphecidae (sphecid wasps)[b]	0.01

[a] Invertebrates were collected in 3.8-L activity traps suspended in the water column for 24 h, one per pond, per month. Collections were June–October 1990 and March–May 1991 for 12 ponds, and July 1991 for 3 radioactive ponds.

[b] Individuals found were mostly or exclusively terrestrial.

Acari ($P = .01$), and Baetidae ($P = .01$). Numbers of Oligochaeta ($P = .44$), Eucopepoda ($P = .50$), Ostracoda ($P = .09$), Corixidae ($P = .08$), Dytiscidae ($P = .54$), and Chironomidae ($P = .70$) collected were not significantly different between sewage and industrial ponds.

Invertebrate numbers in pond NRFi, which had a high mercury content, were compared to those in the remaining industrial ponds, where mercury was not detected. Samples from NRFi contained more Chironomidae ($P = .02$) and Oligochaeta ($P < .01$), and fewer Chydoridae ($P = .03$) and Ostracoda ($P = .03$) than ponds ANLi, TRAi, and CTFi. Numbers of Rotifera ($P = .10$), Daphnidae ($P = .10$), Eucopepoda ($P = .10$), Acari ($P = .15$), Baetidae ($P = .55$), Corixidae ($P = .07$), Notonectidae ($P = .45$), and Dytiscidae ($P = .07$) were similar between the pond with mercury and those without.

DISCUSSION

Wastewater ponds at INEL were nutrient-rich, especially sewage ponds. Organic enrichment may be the cause of high abundance and low number of invertebrate taxa found. Species richness at sewage ponds was similar to that at industrial ponds. However, species composition differed between sewage and industrial ponds. Differences were probably due to the greater organic enrichment in sewage ponds.

Activity trap samples from INEL ponds contained fewer invertebrate taxa than comparable samples from natural waters (Gordon et al.

TABLE 4. Number of aquatic invertebrates per collection (activity trap set for 24 h) from radioactive waste ponds at INEL, Idaho, July 1991[a].

Taxa	CPPir2[b] (n = 1)	TRAr (n = 1)	TSFir (n = 1)
Daphnidae	94	1	59
Chydoridae	0	0	129
Eucopepoda	35	0	818
Ostracoda	5	0	1620
Amphipoda	0	0	1
Baetidae	2	0	0
Corixidae	1	5	0
Dytiscidae	0	6	4
Chironomidae	7	0	18

[a]Data from radioactive waste ponds were not analyzed with those from sewage and industrial ponds because only one sample was taken from radioactive ponds.

[b]CPPir2 = Idaho Chemical Processing Plant east percolation pond (industrial and radioactive), TRAr = Test Reactor Area warm waste pond (radioactive), TSFir = Technical Support Facility disposal pond (industrial and radioactive).

1990, Neckles et al. 1990). Dominant taxa collected from study ponds were similar to dominant taxa collected in activity traps at natural wetlands in Nebraska (Gordon et al. 1990) and Manitoba (Neckles et al. 1990), with the exception of Culicidae, Turbellaria (Neckles 1990), and Gastropoda (Gordon et al. 1990, Neckles et al. 1990), which were not collected from wastewater ponds. In our study fewer taxa per sample were collected compared to activity trap samples from seasonal wetlands (Cowardin et al. 1979, Neckles et al. 1990); seasonal wetlands, like organically enriched systems of sewage ponds, tend to have low invertebrate taxa diversity (Wiggins et al. 1980).

The reduced number of taxa in wastewater ponds may be due to lack of emergent vegetation in most ponds. Odonate families Libellulidae and Lestidae, which were collected by Gordon et al. (1990) but not from wastewater ponds, are commonly associated with vascular hydrophytes (Merritt and Cummins 1984). Vegetation has been found to be correlated with macroinvertebrate species richness (Gilinsky 1984).

Another possible cause of low species richness in wastewater ponds is high organic waste content. Streams and wetlands receiving organic waste typically exhibit low invertebrate taxa diversity (Olive and Dambach 1973, Brightman and Fox 1976, Kondratieff and Simmons 1982, Kondratieff et al. 1984, Victor and Dickson 1985, Pearson and Penridge 1987). Hilsenhoff (1988) assigned arthropod families from streams in the Great Lakes region a tolerance value from 0 (lowest tolerance to organic pollution) to 10 (highest). Eleven of the families for which Hilsenhoff (1988) presented tolerance values were found in INEL ponds, and only 2 had tolerance values of less than 4. Those 11 families and tolerance values are as follows: Aeshnidae and Tipulidae (3), Baetidae, Elmidae, and Leptoceridae (4), Ceratopogonidae (6), Caenidae (7), Chironomidae and Talitridae (8), Coenagrionidae (9), and Psychodidae (10). The two families with a 3 tolerance rating were represented by only single specimens in INEL wastewater ponds.

Low invertebrate diversity in industrial ponds may be caused by organic or chemical constituents. Although nutrients in industrial waste ponds were within ranges found in natural waters, most industrial ponds at INEL would be considered eutrophic (Wetzel 1983). Additional organic enrichment in sewage ponds did not affect species richness compared to industrial ponds; however, species composition (%) was different between the two pond types. Metal and saline pollution has also been found to decrease aquatic invertebrate diversity (Savage and Rabe 1973, Seagle et al. 1980, Euliss 1989).

In most instances, the seven heavy metals tested did not occur in concentrations great enough to affect aquatic life. Only mercury was found at concentrations over chronic exposure levels. At concentrations below chronic levels, freshwater organisms should show no chronic toxic effects (U.S. Environmental Protection Agency 1987). Chydoridae and Ostracoda were scarcer, and Chironomidae and Oligochaeta more abundant, in samples from pond NRFi, wherein mercury was detected. Other toxins may occur in the water, and no other ponds with elevated mercury concentrations were available for comparison. Therefore, we do not know if mercury caused the difference detected.

Although species richness of INEL ponds was low, comparison with natural wetlands (Gordon et al. 1990, Neckles et al. 1990) revealed that study ponds exhibited high invertebrate abundance. Of the taxa that wastewater pond and Nebraska wetland collections had in common, wastewater pond samples contained higher densities of all except Gyrinidae, Ceratopogonidae, and Hirudinea (Gordon et al. 1990). Gyrinidae and Ceratopogonidae were collected in almost identical amounts, and Hirudinea were more abundant in Nebraska

TABLE 5. Median and maximum ( )[a] number of aquatic invertebrates per collection (activity trap set for 24 h) from sewage and industrial waste ponds at INEL, Idaho, 1980–1991. The 12 most abundant taxa are presented.

	Sewage ponds[b]								Industrial ponds			
Taxa	ANLs1 ($n = 8$)[c]	ANLs2 ($n = 7$)	CPPs1 ($n = 8$)	CPPs2 ($n = 8$)	CPPs3 ($n = 8$)	CPPs4 ($n = 8$)	TRAs ($n = 6$)	NRFs ($n = 8$)	ANLi ($n = 8$)	TRAi ($n = 6$)	NRFi ($n = 8$)	CTFi ($n = 8$)
Rotifera	0(47282)	0(15)	2.5(6300)	0(4300)	0(1350)	161(5350)	131.5(1700)	0(36150)	0(0)	0(0)	0(60)	0(0)[d]
Daphnidae	80(142)	8331(28302)	861.5(9428)	656(3324)	874(4799)	236.5(5800)	35.5(1824)	79(523)	282(8770)	0(3)	32.5(95)	18(253)[d]
Notonectidae	0(2)	0(7)	0(0)	0(0)	1.5(10)	0.5(4)	0(0)	0(7)	0(1)	0(0)	0(1)	0(0)[d]
Oligochaeta	0(0)	0(0)	0(1)	0(0)	0(0)	0(0)	1(300)	0(0)	0(0)	0(0)	0.5(187)	0(0)[e]
Eucopepoda	0(2)	0(5)	378.5(1794)	32.5(549)	20(631)	46.5(1218)	112.5(700)	0(3)	57(455)	0(2)	0.5(105)	347(947)[e]
Ostracoda	0(3)	0(107)	58.5(5376)	10.5(100)	2.5(562)	0(16)	12(700)	0(1)	120(711)	152(441)	0(6)	8.5(16900)[e]
Corixidae	1(49)	68(314)	0.5(26)	2.5(8)	15(800)	30(450)	2.5(50)	21(118)	2.5(35)	0(0)	0(0)	2.5(51)[e]
Dytiscidae	0(4)	0(3)	0(4)	0(0)	1(4)	0(1)	0.5(2)	0(1)	0(7)	0(1)	0(0)	0(2)[e]
Chironomidae	0(3)	1(7)	1(150)	2(6)	4.5(12)	2(11)	0.5(248)	1(19)	0(3)	0(0)	4(27)	1(240)[e]
Chydoridae	0(0)	0(0)	0(700)	0(0)	0(0)	0(0)	0(0)	0(0)	1(1950)	0(0)	0(0)	212(3734)[f]
Acari	0(1)	0(1)	0(0)	0(1)	0(0)	0(0)	0.5(1)	0(1)	0(4)	0(0)	0(2)	8.5(73)[f]
Baetidae	0(1)	0(1)	0(50)	0(3)	0(14)	0(0)	1(97)	0(0)	1.5(14)	0(0)	0(25)	18(167)[f]

[a] Means are not given because data are nonparametric. Minimums were >0 in only six instances and >6 twice.

[b] ANLs1 and ANLs2 = Argonne National Laboratory—west sewage ponds, CPPs1-4 = Idaho Chemical Processing Plant sewage ponds, TRAs = Test Reactor Area sewage ponds (TRAs1 and TRAs2 contained water alternately), NRFs = Naval Reactors Facility sewage pond, ANLi = Argonne National Laboratory—west industrial waste pond, TRAi = Test Reactor Area north and south cold waste ponds (industrial—contained water alternately), NRFi = Naval Reactors Facility industrial waste ditch, CTFi = Containment Test Facility disposal pond (industrial).

[c] Samples were collected once per month: ANLs1, CPPs1-4, NRFs, ANLi, NRFi, and CTFi, June–October 1990 and March–May 1991; ANLs2, June–October 1990 and April–May 1991; TRAs, August–October 1990 and March–May 1991; TRAi, July–September 1990 and March–May 1991.

[d] Median test shows numbers collected from sewage ponds are higher ($P \leq .05$) than numbers collected from industrial ponds.

[e] Median test shows numbers collected from sewage ponds are not different ($P > .05$) from numbers collected from industrial ponds.

[f] Median test shows numbers collected from sewage ponds are lower ($P \leq .05$) than numbers collected from industrial ponds.

wetlands, compared to our study ponds (Gordon et al. 1990). Also, in our study, more Cladocera and Ostracoda were collected compared to activity trap samples from seasonal wetlands (Neckles et al. 1990), which tend to have a high invertebrate abundance (Wiggins et al. 1980). Nutrient-polluted natural waters also have invertebrate communities containing many individuals of a few species (Brightman and Fox 1976, Lubini-Ferlin 1986); Brightman and Fox (1976) attribute this partially to a reduction in competition from pollution-intolerant forms.

High invertebrate growth and abundance have been associated with high algal productivity (Wallace and Merritt 1980, Richardson 1984), which in turn has been associated with high phosphorus and nitrogen concentrations (Liao and Lean 1978, Wetzel 1983). Most INEL wastewater ponds were eutrophic or highly eutrophic (Wetzel 1983). Therefore, wastewater ponds, which are higher in nutrients than natural wetlands, would be expected to produce more invertebrate biomass.

The absence of fish in study ponds probably also contributed to high invertebrate densities. Fish have been shown to decrease aquatic invertebrate densities (Gilinsky 1984). For most taxa, collections from industrial ponds also had more individuals than collections from natural systems (Gordon et al. 1990, Neckles et al. 1990), even though industrial ponds were not as nutrient-rich as sewage ponds.

In certain systems a large abundance of invertebrates has also been attributed to a paucity of insect predators (Brightman and Fox 1976, Williams 1985, Dodson 1987). However, several predaceous taxa were collected from waste ponds, most notably Dytiscidae and Notonectidae. Because these taxa were collected in greater numbers from wastewater ponds than from natural wetlands (Gordon et al. 1990), and because Notonectidae were most numerous in sewage ponds where many prey taxa were also most numerous, we surmise the large number of invertebrates collected from waste ponds resulted mostly from a reduction in competition from pollution-intolerant taxa, high algal productivity, and the absence of fish, rather than from lack of invertebrate predation.

Comparison of our results on water column invertebrates with other studies of sewage ponds is limited due to a scarcity of published papers. Porcella et al. (1972) noted large populations of *Daphnia* in a reservoir fed mostly by treated sanitary wastewater. Daphnidae, Rotifera, and Notonectidae were more common in INEL sewage ponds than in industrial ponds. All three species, as well as Oligochaeta, Eucopepoda, Ostracoda, and Corixidae (Sinclair 1975), are common inhabitants of sanitary wastewater. Oligochaeta, Eucopepoda, Ostracoda, Corixidae, and Chironomidae were abundant in sewage ponds, but not more so than in industrial ponds. Cladocera, Eucopepoda, Ostracoda, Corixidae, and Chironomidae were also common in evaporation ponds in California, which contain salts and heavy metals (Euliss et al. 1991).

Invertebrate communities in INEL sewage ponds differed from those in organically polluted streams. However, in making these comparisons we note that our sampling methods did not target benthic organisms. In nutrient-enriched stream reaches, oligochaetes and chironomids are dominant (Duda et al. 1982, Pearson and Penridge 1987, Crawford et al. 1992), but we found no difference in numbers between sewage and industrial ponds. Some chironomid species (Kownacki 1977) and oligochaete families (Lewis 1986) are characteristic of clean waters, and it is possible the species inhabiting sewage ponds differed from those in industrial ponds. Ostracoda have also been described as pollution tolerant (Kownacki 1977), but we found no difference in their numbers at the .05 level of significance; at the .10 level, sewage pond samples contained more ostracods. Baetidae may be either pollution tolerant (Savage and Rabe 1973, Victor and Dickson 1985) or intolerant (Kownacki 1977) depending upon the species. We found more Baetidae in industrial ponds, indicating they, as well as Chydoridae and Acari which were also more abundant in industrial pond samples, may be less tolerant of low oxygen concentrations than the other common taxa.

Taxa found in greater abundance in sewage ponds than in industrial ponds were those that could take advantage of the unique and difficult living conditions. Eutrophic waters typically exhibit lower dissolved oxygen concentrations and greater fluctuations in dissolved oxygen and pH than less organically enriched waters. Some cladoceran species can form hemoglobin when dissolved oxygen concentrations are low; thus, oxygen levels are rarely a limiting factor (Pennak 1989). The same is true of rotifers; certain genera are capable of withstanding anaerobic conditions for a short time and very low oxygen concentrations for extended periods (Pennak 1989). Since Notonectidae breathe at the water surface (Merritt and Cummins 1984), they are unaffected by dissolved oxygen concentrations. Most Cladocera are less affected by pH fluctuations than some taxa because they typically occur over a wide pH range (Pennak 1989). If pH levels are too high or too low, Cladocera and Rotifera can withstand temporarily unfavorable environmental situations by producing resting eggs that are resistant to adverse chemical conditions. Under more favorable-conditions, Cladocera and Rotifera life cycles allow them to respond quickly to improving conditions (Pennak 1989).

Regarding the feeding habits of taxa that were more abundant in sewage ponds, Notonectidae were possibly taking advantage of the reduced competition from other predators. Both rotifers and *Daphnia* are omnivorous and feed on any suitable-sized food particle; therefore food was abundant for them in sewage ponds (Sinclair 1975). *Daphnia* can alter their body structure in response to algal concentrations, which is thought to be a mechanism for surviving algal blooms (Pennak 1989). Thus, while conditions in sewage ponds are hostile to many species, those that can tolerate the conditions flourish due to an abundant food supply and the absence of fish.

In summary, wastewater ponds had low invertebrate diversity, which we attribute to lack of vegetation and inability of many species to withstand the environmental conditions. Wastewater ponds also had high invertebrate abundance, which we attribute to reduction of competing taxa, organic enrichment, and absence of vertebrate predators. There was no indication that heavy metal concentrations were high enough to reduce water column invertebrate concentrations in most ponds.

High invertebrate concentrations in INEL wastewater ponds provided an abundant food source for many bird species, migratory and resident, which used INEL wastewater ponds. Bacteria, protozoa, and algae are important in waste treatment because they reduce the organic load of wastewater and convert waste into a form useable by organisms in the receiving water body (Goulden 1976). In systems like some at INEL where water loss is through evaporation, all waste processing occurs in the pond. Zooplankton are also important in waste elimination and transfer (Goulden 1976, Patrick 1976, Bogatova and Yerofeyeva 1980). Other aquatic invertebrates that consume algae or bacteria, or feed on zooplankton, and are then eaten by birds also influence the reduction and transformation of organic waste and its dissipation out of the system.

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GROWTH AND REPRODUCTION IN AN ALPINE CUSHION PLANT: *ASTRAGALUS KENTROPHYTA* VAR. *IMPLEXUS*

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ABSTRACT.—A two-year field experiment was conducted to investigate factors hypothesized to affect the reproductive potential of *Astragalus kentrophyta* var. *implexus* and to test the importance of trade-offs between growth and reproduction in this species. Levels of mineral nutrients, water, herbivory, and competition were manipulated. Seed output and growth of individuals in treatment groups were compared against control plants. Neither water nor mineral nutrients alone were shown to affect growth or reproduction. Herbivory was shown to be similarly unimportant in affecting growth and reproduction. Competition with other species influenced growth but not reproduction. No significant trade-offs between growth and reproduction were detected within years. However, there did appear to be a trade-off between these major fitness components when compared between years.

Key words: Astragalus, *alpine, competition, fecundity, trade-off,* White Mountains.

The impact of resource availability on the reproductive output of plants is well established (Harper 1977, Schoener 1983, Fowler 1986, Welden and Slausen 1986). Plants may experience resource limitation as a result of competition (inter- or intraspecific) or poor habitat quality. Resource limitations can also occur when a portion of a plant's photosynthetic organs are removed (e.g., by herbivory), damage which clearly interferes with the plant's ability to provision its offspring (Marquis 1991). A number of authors (Cody 1966, MacArthur and Wilson 1967, Harper 1977, Grime 1979, Tilman 1982, Weiner 1988, 1990) have considered the ecological consequences of resource limitation for individuals and populations and have described various strategies that plants might be expected to pursue to optimize the allocation of limited resources.

This study tests whether the availability of resources limits the fecundity of *Astragalus kentrophyta* Gray var. *implexus* (Canby) Barneby (hereafter, simply *A. kentrophyta*) and to what extent trade-offs between growth and reproduction might influence patterns of reproduction observed in this species. *A. kentrophyta* is an alpine cushion plant indigenous to high elevations throughout the Intermountain West of North America (Barneby 1964).

Many lines of evidence suggest that reproduction in *A. kentrophyta* might be resource limited. Experiments involving other organisms from this habitat have shown that availability of resources influences the competitive ability and distribution of species (Wright and Mooney 1965, Mooney 1966, Marchand 1973), though this is not generally true of all alpine habitats (Korner 1989). Second, standing biomass and percent cover are substantially lower on dolomitic soils than on adjacent sandstone- and granite-derived substrates, suggesting that plants on the dolomite barrens might be relatively resource limited (Mooney 1966, Owen 1991). Third, *A. kentrophyta* plants routinely abort the majority of flowers they produce each year (Owen 1991), a pattern that has been attributed to resource limitations in a broad spectrum of species (Lovett Doust and Lovett Doust 1988).

An experiment was designed (1) to test whether there are resource constraints on the reproduction and growth of *A. kentrophyta* and (2) to assess the interactions between two major components of fitness (i.e., growth and reproduction) under different regimes of resource availability. To do this, a factorial field experiment was established in which separate groups of plants would receive either (1) water or (2) nutrient supplements, (3) protection from herbivory, or (4) relief from the potentially competitive influence of neighbors.

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STUDY AREA

The study was conducted on the alpine dolomite barrens of Sheep Mountain Pass above the Patriarch Grove bristlecone pine forest, in the White Mountains of Mono County, CA. Elevations at the site range from 3535 m (11,600 ft) to 3660 m (12,000 ft), and topographic relief of the site is minimal. In the White Mountains *A. kentrophyta* occurs only on dolomitic soils (Lloyd and Mitchell 1973, Hall 1991).

Weather data were obtained from the White Mountain Research Station, Mt. Barcroft Laboratory, located 6 km north of the study site at an elevation of 3800 m. Soils on the dolomite barrens have a high cation exchange capacity and are depauperate in nitrogen, phosphorus, and potassium (Mooney et al. 1962, Wright and Mooney 1965, Brayton and Mooney 1966, Mooney 1966, Marchand 1973, 1974). The moisture-holding capacity of dolomite-derived soils is equivalent to that of adjacent granitic soils (Mooney et al. 1962, Wright and Mooney 1965, Marchand 1973). Vegetation of the White Mountains is generally xerophytic; this trend is especially prevalent on the dolomite barrens (Lloyd and Mitchell 1973).

MATERIALS AND METHODS

In June 1989, 195 healthy *A. kentrophyta* plants were selected randomly from within an area of approximately 0.2 ha. Decadent (senescent) plants were disqualified from inclusion in this experiment. The specific location of the site was chosen for its apparent homogeneity with respect to soil physical characteristics, vegetation, and topographic profile. Plants were randomly allocated to five treatment regimes: (1) 50 plants were provided with three separate 1-L applications of water during the 1989 growing season. Plants were watered during the driest part of the summer (4 July, 2 August, and 19 August) to maximize the beneficial impact of the treatment. Water was applied slowly (to maximize infiltration) in a radius of 12.5 cm around each plant. This treatment supplied 6.1 cm of moisture to each plant. Expected precipitation for the three-month growing season is 8.7 cm (Pace et al. 1968). The 1989 summer precipitation was 1.1 cm. This treatment group will be referred to as "Water." (2) Another 50 plants received supplemental nutrients. These plants were given approximately 17 g of a balanced general-purpose fertilizer (Scott's All-Purpose Builder, 12:10:12 N:P:K), providing each plant with 2.0 g N (in the form of ammoniacal nitrogen, ureas, and water soluble nitrogen), 1.7 g P (from phosphoric acid, P_2O_5), and 2.0 g K (from soluble potash, K_2O). These quantities are equivalent to application rates of 13.8, 11.7, and 13.8 kg ha^{-1}, respectively. A balanced fertilizer was chosen because experiments by Chambers et al. (1987) and Shaver and Chapin (1980) have shown that plants in cold environments respond most vigorously to resource augmentation with fertilizer containing a balance of essential nutrients. The dry fertilizer was scattered in an approximately 2-cm-wide ring around the perimeter of each test plant. Summer seasonal precipitation in 1989 was apparently sufficient to solubilize the fertilizer and deliver it to the soil profile, as the granules had completely disappeared from the surface in approximately one month. This treatment group will be referred to as "Fertilized." (3) A third treatment was designed to protect plants from herbivory and predation on flowers and young fruits. Two locally common insects habitually consume the reproductive parts of *A. kentrophyta*. The more common of these insects, a darkling beetle (Tenebrionidae: Coleoptera), consumes flowers. Larvae of a locally common Lycinid butterfly species (Lycaenidae: Lepidoptera) occasionally consume immature *A. kentrophyta* fruits. "Tangle-foot" brand sticky-trap was applied in a circle around each of 25 plants to exclude potential herbivores. Tanglefoot barriers were repaired as needed. This treatment group will be called "No Predation." (4) The fourth treatment sought to relieve a group of 20 *A. kentrophyta* plants from neighborhood competition. A 0.25-m-radius circle around a central target *A. kentrophyta* plant was cleared of all other plants by cutting them off at ground level. This method minimized ground surface disturbance. Clearings were 0.2 m^2 in area. The average number of neighbors (ramets) removed was 63 (mostly tillers of *Poa rupicola*), covering an average of 15% of the ground surface. Excavations of *A. kentrophyta* plants show that its roots grow straight downward into the soil with minimal lateral root spread (Owen 1991). Roots of the target plants were therefore thought to be well isolated from interactions with actively assimilating roots of other plants. Plants clipped in the cleared areas were trimmed if they resprouted. Plants in this treatment group are referred to as the "Target" group. (5) A final group of 50 unmanipulated plants was marked as a "Control" group. Size of the experimental groups was based on an analysis of expected variances in responses to the treatments; lower expected variances require smaller necessary samples (Sokal and Rohlf 1981).

Plant sizes (cushion area) were measured and recorded on 23 June 1989, shortly after initiation of growth for the season. Treatments were initially applied on 4 July 1989. In September 1989 all plants were remeasured, and the entire fruit and seed crop produced by each of the 195 plants was harvested. Since *A. kentrophyta* forms a tight cushion that never exceeds 1 cm in height and seeds are not released from the plant before the end of the growing season, there was great confidence that the entire seed crop of each individual was retrieved. In early June 1990 I again measured the area of all plants just as they were initiating growth for the season. Fertilized and Water treatments were not repeated in 1990 so as to evaluate the potential for lags in the effectiveness of resource supplementation. Tanglefoot barriers were maintained during 1990 to test for interannual variation in the effects of herbivores and predators. Clear zones around Target plants were maintained in 1990. All plants were allowed to grow through the season, and in September 1990 all 195 plants were remeasured and all fruits and seeds harvested. No attempt was made to quantify flower production, but previous experience (Owen 1991) had shown that seed production is a significant function of flower production (Owen 1991). Flowers, when aborted, are dropped at a very early age (Owen 1991) and probably represent a minimal per-unit cost in resources to the plant (Bookman 1983, Stephenson 1984). Therefore, the cost of flowers should be proportional to a plant's seed output and can safely be disregarded for the purpose of this work. Fruits and seeds were cleaned and separated in the laboratory, counted, and weighed.

RESULTS

Weight of individual reproductive structures (seeds and fruits) was independent of total numbers of those items produced per plant in both years (Table 1). Average seed and fruit weights were significantly correlated ($R = .429$ in 1989, $R = .443$ in 1990). There were no significant differences between treatment groups for the weight of individual seeds or fruits (results not presented). Because seed production is well correlated with other possible measures of fitness in *A. kentrophyta* and weights of those seeds are independent of the numbers of reproductive structures produced on a plant (Table 1), seed output was used as an index of total reproductive effort.

In a comparison of slopes of regression analyses, growth was a significant function of plant size in both 1989 and 1990 (Table 2), though the relationship was weaker in 1990. The weight of individual seeds and fruits was independent of seasonal growth (Table 2). The amount of growth across years was significantly but poorly correlated.

TABLE 1. Correlation matrix for selected demographic traits. Values above the diagonal are correlation coefficients (R) based on 1990 data; those below the diagonal are derived from 1989 data.

	Seeds produced	Seed weight (average)	Seed weight (total)	Fruits produced	Fruit weight (average)	Fruit weight (total)	Reproductive weight (total)
Seeds produced**	1	.003	.976*	.964*	.143*	.920*	.966*
Seed weight (average)	.042	1	.139*	–.001	.433*	.081*	.115*
Seed weight (total)	.977*	.200*	1	.945*	.229*	.937*	.987*
Fruits produced**	.963*	.024	.033*	1	.106	.963*	.968*
Fruit weight (average)	.136*	.429*	.215*	.074	1	.289*	.260*
Fruit weight (total)**	.943*	.120*	.949*	.952*	.284*	1	.981*
Total reproductive weight**	.973*	.1656*	.989*	.954*	.249*	.985*	1

*Kendall Rank Correlation is significant at $P < .05$.

**Treatment differences noted with one-way ANOVA. These differences do not affect the magnitude of significance of the correlations.

TABLE 2. Slopes of regressions for selected demographic traits on growth in 1989 and 1990 using the total data set (i.e., not partitioned by treatment). Where the overall regressions are not significant, there were also no treatment differences.

	Growth in 1989	Growth in 1990
Growth in 1990	.168*	—
Plant size	.340*	.110*
Seed weight	–.038	–.054
Fruit weight	.035	.036

*Regressions are significantly positive ($P < .05$). One-way ANOVAs suggest differences between treatment groups for values of these traits ($P < .05$).

TABLE 3. Result of an ANCOVA on seed production and growth by treatment group. The covariate is plant size. The treatments are those listed in the text (see also Table 4).

	Covariate		Treatment	
	F	*P*	F	*P*
1989 Seed production	37.164	<.001	1.358	.25
1990 Seed production	39.818	<.001	1.854	.12
1989 Growth	27.207	<.001	0.822	.583
1990 Growth	0.893	.346	2.453	.047

Seed production (square root transformed) was a positive linear function of plant size. Overall values of R^2 for regressions of seed production on plant size were .206 in 1989 and .182 in 1990. Slopes of individual regressions for each treatment for seed production on plant size did not differ from the slope for control plants.

Plant size was a minor but important factor influencing both growth and reproduction in *A. kentrophyta* and indicates that size should be considered as a covariate in an analysis of variance of treatment effects in this experiment. Analyses of covariance (ANCOVA) and experimental results are presented in Tables 3 and 4, respectively. Plant size was a significant covariate in three of four analyses. There were no differences among treatment groups in seed production (reproduction) for either year. Growth did not differ among treatment groups in 1989, but there was a significant difference between groups in 1990 ($P = .047$). A protected least-significant-difference (LSD) test indicates that growth in the Target group was greater than that of individuals in other treatment groups (Table 4).

Table 5 gives the results of two-tailed *t* tests comparing mean reproduction and growth across years within treatment groups. There were no significant differences for seed production among treatment groups between 1989 and 1990. Average size for plants in 1990 was consistently significantly greater than the size of the same plants the previous year (i.e., on average, plants grew larger over the course of the experiment). The No Predation treatment grew significantly less in 1990 than 1989, whereas plants in the Target group grew significantly more in 1990. There were no significant differences in growth across years for plants in the Control, Fertilized, or Water groups.

A series of simple linear regressions was used to compare seed production with growth to test for the presence of a trade-off between these two primary components of fitness. When the data are corrected for the fact that larger plants are inherently more capable of producing more flowers and fruits, the analysis finds no significant differences among treatment groups (by virtue of overlapping 95% confidence intervals); and, therefore, no trade-off between growth and reproduction within a given year was detected.

To compare trade-offs across years, the ratio of 1990 to 1989 data was used (Table 5). This provides a number >1.0 when 1990 data values exceed 1989 values; the converse is true when results are <1.0. Seed production was greater in 1990 than in 1989 regardless of treatment group. In contrast, growth in 1990 was less than that experienced in 1989 with the notable exception of Target plants. The results can be interpreted as evidence for a trade-off between growth and reproduction. They indicate that, in general, increased seed production is associated with decreased growth. Furthermore, plants may be relieved of trade-off constraints by removing competitors, which should increase availability of mineral resources to the remaining (target) plant.

DISCUSSION

Resource supplementation or alleviation of resource competition did not significantly influence the reproductive output of *A. kentrophyta*. Instead, seed production was more closely related to the individual's past record of seed output (Tables 1, 3, 5). Plants that produced many seeds in 1989 tended to produce many seeds in 1990, regardless of treatment. Growth, while similarly unresponsive to the addition of single resources, increased significantly when potential competitors were removed (Tables 4,

TABLE 4. Treatment means (SD) in both 1989 and 1990 for important demographic traits.

	Control	No bugs	Fertilized	Water	Target
1989 Seed production	25.8 (25.2	16.1 (11.8)	30.6 (24.5)	25.1 (22.2)	44.2 (41.4)
1990 Seed production	32.2 (32.28)	20.5 (16.7)	39.7 (37.3)	30.7 (27.9)	54.5 (58.4)
1989 Plant size	5997.1 (2851.7)	4594.6 (1871.8)	6833.9 (2892.7)	6333.2 (2891.4)	7683.2 (3683.8)
1990 Plant size	7247.3 (3128.8)	5596.3 (2156.6)	7934.0 (3242.6)	7418.2 (3627.4)	8393.0 (4159.9)
1989 Growth	1478.4 (1329.7)	1530.0 (987.7)	1772.1 (1634.2)	1797.9 (1486.9)	1503.1 (988.6)
1990 Growth*	1156.1 (1529.9)	808.4 (1000.4)	1587.8 (2044.5)	1395.0 (1760.3)	2433.2 (1749.0)

*Growth in 1990 varied significantly among treatments (see Table 3). The Target groups grew more, on average, than did plants in any other treatment group. No other differences were significant.

5). These results differ from those of Wright and Mooney (1965), Mooney (1966), and Marchand (1973), which show that mineral nutrients were the primary factors limiting other species that occur on dolomite in the White Mountains (*Artemisia tridentata*, two *Erigeron* species, and *Lupinus argenteus*, respectively). Korner (1989) reports that the effect of fertilization on the growth of species from nutrient-poor environments is often difficult to detect. He does not cite studies that address the relationship between growth and reproduction in nutrient-supplementation experiments.

The addition of mineral nutrients or water alone may have been insufficient stimuli for *A. kentrophyta* to increase either reproduction or growth if both factors were limiting. Multiple limiting factors have been reported in a variety of species (Harper 1977) and are specifically predicted by Tilman's (1980, 1982) models of optimal resource consumption. That there may be multiple resource limits to *A. kentrophyta* growth and reproduction is supported by the response of *A. kentrophyta* to the removal of competitors in this study.

Tanglefoot barriers were very effective at excluding ground-moving herbivores and predators. This was evidenced by the lack of foliar damage or partially eaten fruit and the capture of many insects in the traps. Flowers of *A. kentrophyta* are produced in sufficient excess to buffer individuals against the levels of flower and fruit predation observed in this population.

Growth in *A. kentrophyta*, as has been reported for a number of species from arid regions throughout the world (Fonteyn and Mahall 1981, Robberecht et al. 1983, Ehleringer 1984, Parker and Salzman 1985, Shaw 1987, Manning and Barbour 1988, and Chapin et al. 1989), is most sensitive to the proximity of its neighbors. It is unclear, however, why reproduction among such species is rarely similarly influenced (as is the case with *A. kentrophyta*). The buffering of fitness components against environmental stochasticity is characteristic of density-vague demographics as described by Strong (1986). Under density-vague conditions, selection favors demographic functions with indeterminate functional thresholds. That is, current allocation decisions are only loosely linked to current environmental conditions (Strong 1986).

Trade-offs between growth and reproduction within years were not observed in this experiment under any conditions. A weak trade-off between growth and reproduction was identified in most treatment groups when data were compared across years (Table 5). It is of great interest that the Target group alone experienced an increase in both seed production and growth in 1990 compared to 1989 values (and thus did not experience a trade-off). The absence of well-defined trade-offs between primary components of fitness could be due to one of several reasons. Lack of a discernible trade-off would be noted if resources were not truly limiting. It may also be that growth and reproduction are not co-limiting for this species in this environment. If this were true, factors that influence growth and reproduction are likely to be independent (e.g., one fitness component might be canalized and the other dependent on environmental conditions). Finally, a trade-off between growth and reproduction would not be detected if a resource other than one provided in this experiment were limiting.

Adult *A. kentrophyta* mortality at the Sheep Mountain study site is low, juvenile mortality is extremely high (even though germination

TABLE 5. Cross-year comparisons of fitness components. 1990 values represented as a fraction of 1989 trait values. Values of t and the associated probabilities (P) represent results of two-tailed t tests for differences in values between years. Refer to Table 4 for raw data.

		Control	No bugs	Fertilized	Water	Target
Seed production	90/89*	1.25	1.16	1.32	1.15	1.18
	t	1.41	1.71	1.80	1.39	0.71
	P	.17	.10	.08	.17	.49
Plant size	t	7.06	5.02	4.90	5.05	3.50
	P	<.01	<.01	<.01	<.01	<.01
Growth	90/89*	0.85	0.98	0.56	0.86	2.07
	t	1.13	2.50	0.40	1.42	2.12
	P	.26	.02	.70	.16	.05

*Values listed represent the ratio of 1990 trait values to those of 1989.

tests under controlled conditions show seed viability of greater than 95%), and recruitment is low (Owen 1991). These demographic attributes would certainly favor a strategy that routes resources away from the risky business of reproduction toward growth. The small but consistent portion of *A. kentrophyta*'s annual accumulation of biomass allocated to reproduction guarantees that each plant will probably produce at least a few seeds each year while being able to dedicate most of each season's accumulated resources to growth and survival. That the allocation of resources to reproduction, but not growth, in this species is constant over a broad range of resource availabilities is consistent with a bet-hedging life-history strategy (Kozlowski and Stearns 1989, Philippi and Seger 1989, Stearns 1989).

Resource limitations on organisms are rarely simple or solitary. While fruit and flower predation can be an important limit on fecundity, such an effect was not noted here. Similarly, the reproductive output of plants growing on the Sheep Mountain dolomite barrens would appear to be resource limited, although single resource augmentation had no direct effect on seed production. In combination, however, resources can influence the amount of realized growth that in subsequent years will affect reproduction.

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CALILEUCTRA, A NEW GENUS, AND TWO NEW SPECIES OF STONEFLIES FROM CALIFORNIA (PLECOPTERA: LEUCTRIDAE)

W. D. Shepard[1] and R. W. Baumann[2]

ABSTRACT.—*Calileuctra* is proposed as a new genus in the family Leuctridae, with *Calileuctra ephemera* designated as the type species. All stages of *Calileuctra ephemera* are described. *Calileuctra dobryi* is described in the male and female stages. Both species inhabit the Mediterranean climatic region of California. A phylogenetic analysis of the genera in the family Leuctridae is given, which places *Calileuctra* near the genus *Perlomyia*.

Key words.—Insecta, Plecoptera, Leuctridae, Calileuctra, *description, distribution, phylogeny.*

Both of us have been collecting stoneflies from streams all across California. Several years ago one of us (WDS) collected a small and poorly sclerotized stonefly nymph from an intermittent Napa Valley stream. The male adult that was reared from the nymph could not be determined using existing keys by WDS. The specimen was then given to RWB for identification. His identification kept us collecting at the same site for nine years. The single male specimen was first thought to be a new species in the Asian genus *Rhopalopsole*. However, recent work indicates that the male represents a new genus in the family Leuctridae. Despite extensive searching in surrounding areas, only the Napa Valley population has been found.

A few years after discovery of the first new species, RWB found, in the Natural History Museum of Los Angeles County, a small series of an interesting new leuctrid from the San Gabriel Mountains. Later, two additional females of this species were collected in the Santa Ana Mountains. However, we decided that fresh male specimens were needed before a description could be undertaken.

Keith Dobry, who was doing fieldwork in the Los Angeles area, was encouraged to look for additional specimens of this leuctrid species. He was successful in locating two additional populations, one in the San Gabriel Mountains, the other in the Santa Monica Mountains. This species is known from only four populations, all from mountains surrounding the Los Angeles basin.

Calileuctra, new genus

TYPE SPECIES.—*Calileuctra ephemera,* new species

ADULTS.—Body brownish, weakly sclerotized; setation sparse, except for abundant tiny setae, "clothing hairs" (Figs. 1, 10). Wings macropterous or brachypterous; venation as illustrated (Fig. 3). Prosternum with presternum separate, furcasternum fused to base of triangular basisternum; meso- and metasternum similar except basisternum rectangular (Fig. 2).

MALE.—Tergum IX with posterior border heavily sclerotized and irregularly serrate or dentate; tergum X with posterolateral corners, each with one or two elongate horns projecting posteriorly (Figs. 4, 11); sternum IX projecting posteriorly to cover base of paraprocts, with vesicle broadening posteriorly (Figs. 6, 13); paraprocts fused into a complex, T-shaped, subanal probe, with two ventromedial projections off subanal probe (Figs. 8, 9, 13).

FEMALE.—With weak abdominal sclerotization; sternum VII completely sclerotized; sternum VIII largely membranous; sternum IX completely sclerotized; subgenital plate poorly produced; sternum X incompletely sclerotized (Figs. 7, 14). Cerci one-segmented; elongate in male, poorly sclerotized on sides, apically flat and membranous (Figs. 4, 11); simple in female (Figs. 7, 14).

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NYMPH.—Mature nymph weakly sclerotized; body elongate; setation scarce. Abdominal segments I–VII with membranous pleural fold. Mesosternal Y-ridge with double stem; arms meeting furcal pits at posterior ends. Paraprocts fused basally with no visible suture; sparse setation. Cercal segments each with apical fringe of 10–15 setae; setae approximately one-half length of cercal segments.

DISTRIBUTION.—Napa Valley and Los Angeles basin, CA.

DIAGNOSIS.—Males are best characterized by their unique elongate, flat-topped cerci. Females are characterized by sternum VIII being incomplete, and the lack of a posteriorly projecting subgenital plate. Nymphs are characterized by abdominal segments I–VII having a membranous pleural fold, the subanal lobes having basal fusion but no distinct fusion line, and the cercal segment setae being one-half length of the cercal segment.

ETYMOLOGY.—The prefix *Cali-* was selected to denote California, the origin of the specimens. The suffix *-leuctra* was selected to indicate placement of the genus in the family Leuctridae. Gender of the name is neuter.

KEY MODIFICATION.—Modifications are given for the following identification keys for Nearctic leuctrid genera: Harper and Stewart (1984)—nymphal and adult keys; Stewart and Stark (1988)—nymphal key. Wording, style, and figure citations are as presented in the original keys.

Harper and Stewart (1984)—Nymphal Key

38 (37) Body robust, length less than 8 times width; body conspicuously clothed with hairs about one-fifth the length of middle Ab segment; subanal lobes of mature male a fused, strongly keeled plate, much produced with no posterior notch (fig. 13.44) . . . . *Megaleuctra*

38′ Body more elongate, fine hair pile inconspicuous, appearing naked; subanal lobes of mature male fused one-half to two-thirds length, leaving a notch at tip 38A

38A (38) Subanal lobes fused but with complete suture; apical setae on cercal segments usually less than one-half length of cercal segments . . . . *Perlomyia*

38A′ Subanal lobes basally fused, no suture in basal half; apical setae on cercal segments one-half length of cercal segments . . . . *Calileuctra*

Harper and Stewart (1984)—Adult Key

58 (56) In hind wing, Cu_1 not forked . . . *Calileuctra*

58′ In hind wing, Cu_1 forked 58A

58A (58′) In hindwing, m-cu joining Cu_1 beyond fork of Cu_1 59

58A′ In hindwing, m-cu joining Cu_1 before fork of Cu_1 60

Stewart and Stark (1988)—Nymphal Key

5. Pronotum with no long, marginal setae (Fig. 8.14A); paraprocts of both sexes fused basally, with no distinct medial line of separation 5A

Pronotum with 2–4 long hairs on anterior and posterior margins (Fig. 8.2A, 8.12A); paraprocts of both sexes fused with distinct medial line of separation or slightly separated medially (Fig. 8.2H,I; 8.12H,I) 6

5A. Abdominal segments 1–6 divided by ventrolateral membrane; ENA and SW . . . . *Zealeuctra*

5A′ Abdominal segments 1–7 divided by ventrolateral membrane; WNA . . . . . . *Calileuctra*

Key to Adults of *Calileuctra*

1a Wings macropterous; male with epiproct bifurcate dorsally, tergite IX posteriorly emarginate with two large heavily sclerotized teeth, cerci with apical tooth, tergite X with one tooth on each posterolateral corner, sternite IX with posterior projection broadly rounded; female sternite VII broad with a posteriorly projecting rectangular lobe, sternite VIII membranous . . . . *C. dobryi*

1b Wings brachypterous; male with epiproct with one dorsal hook, tergite IX with single sclerotized posterior plate bearing numerous teeth, cerci without apical tooth, tergite X with two teeth on each posterolateral corner, sternite IX with posterior projection broadly angulate; female sternite VII elongate with lateral constrictions, sternite VIII with two arcuate sclerotized plates. . . . . *C. ephemera*

Calileuctra ephemera, new species

Figs. 1–9

MALE.— General color brown; dark brown pattern as illustrated (Fig. 1). Length of body 4.5 mm. Brachypterous, length of forewing 2.5–3.0 mm; wings light brown, venation similar to the genus *Perlomyia* (Fig. 3). Prothoracic basisternum triangular in shape (Fig. 2). Abdominal tergum IX with posterior border complete, projecting and serrate; tergum X

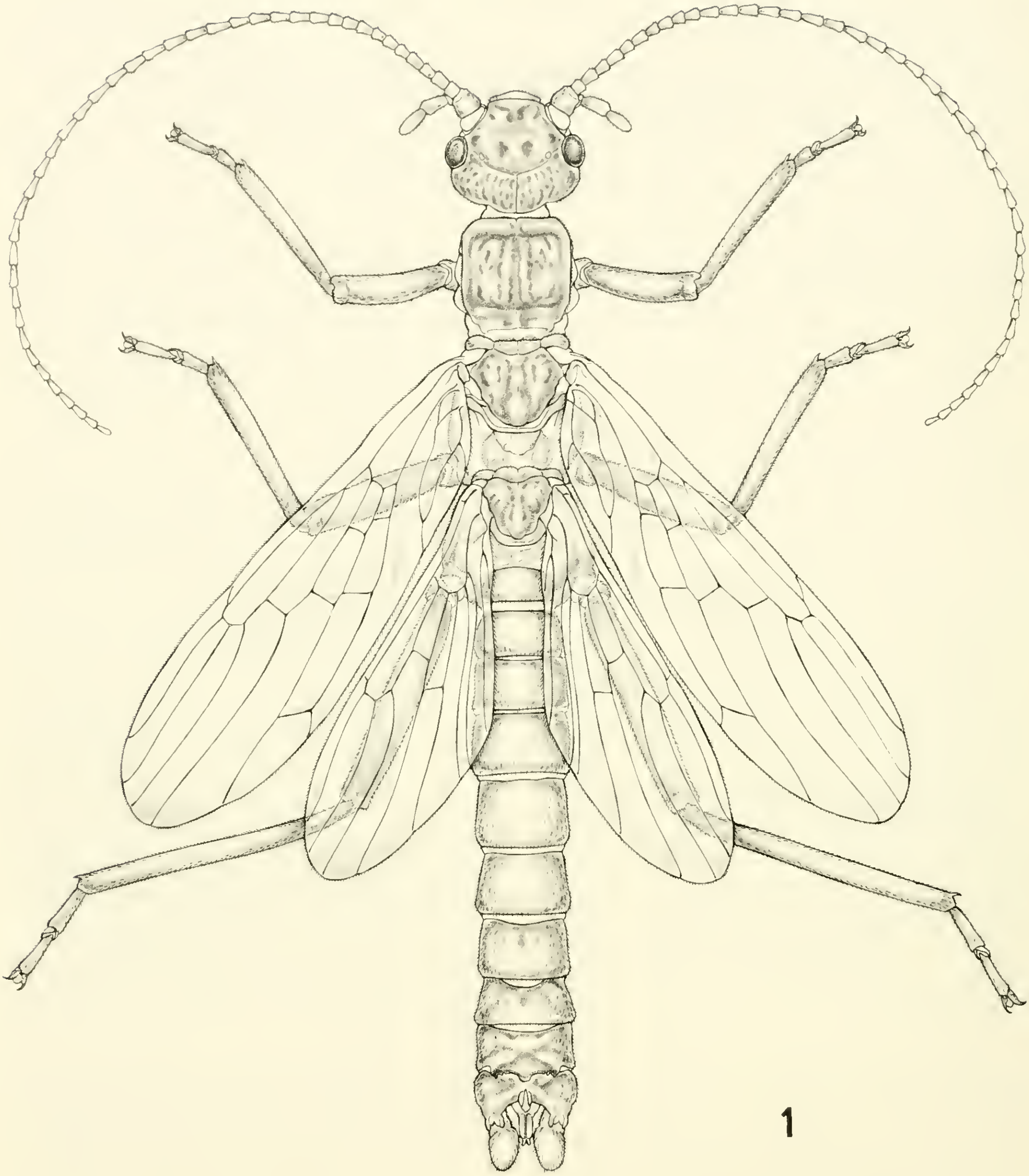
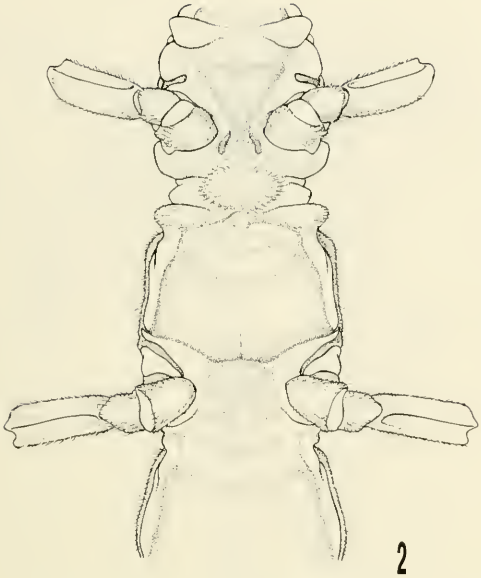


Fig. 1. *Calileuctra ephemera.* Habitus.

incomplete medially, posterolaterally with two elongate projections (Figs. 4, 5). Sternum IX with basal pear-shaped vesicle; posterior border extending to base of subanal probe (Fig. 6). Cerci extending beyond genitalia, with apical membranous area expanded and flattened (Figs. 4, 5, 6). Epiproct small and hook-shaped (Fig. 5). Subanal probe large, elongate, both membranous and sclerotized, expanded near apex (Figs. 8, 9).

FEMALE.— General color and wing venation similar to male. Brachypterous, length of forewing 3.5–4.0 mm. Sternum VII constricted laterally, projecting slightly over sternum VIII; sternum VIII reduced to 2 small arcuate sclerotized plates (Fig. 7).



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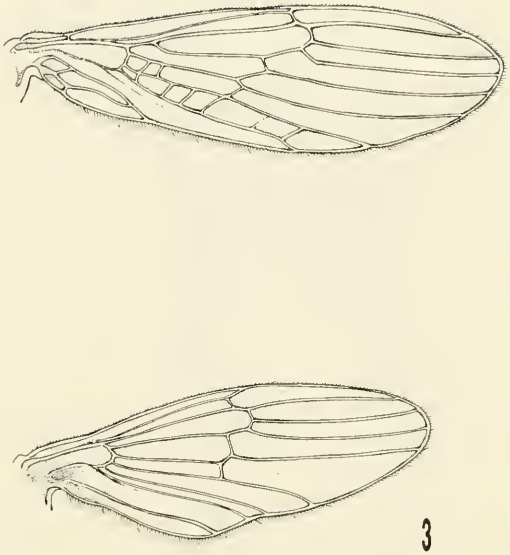

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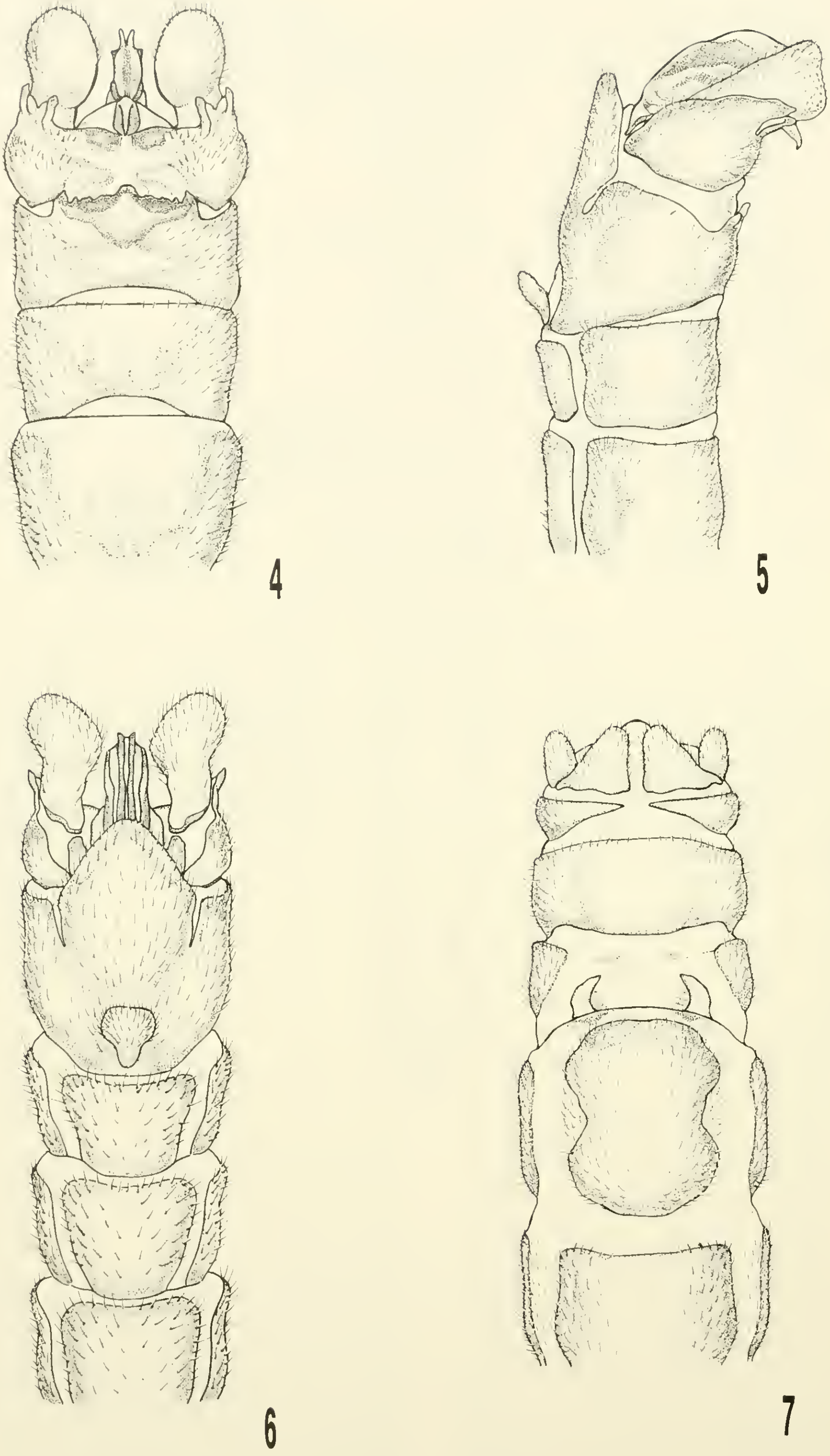
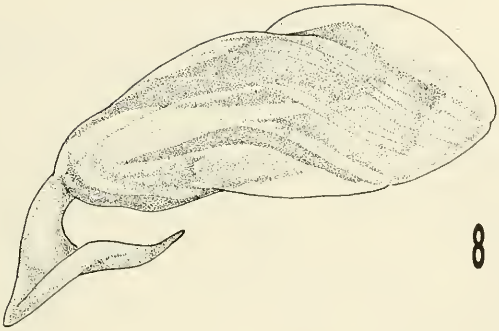
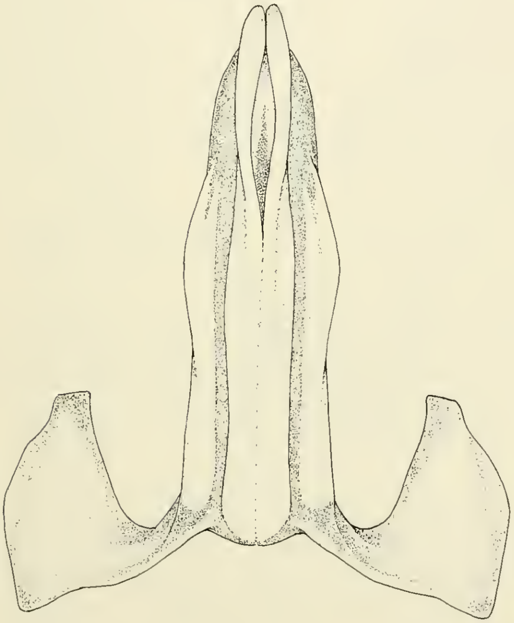
Figs. 2, 3. *Calileuctra ephemera*: 2, ventral view of thorax; 3, wings.

NYMPH.—Body lightly sclerotized; light in color; setation sparse except on labrum, legs, and cerci; size small—7.2 mm long. Head slightly broader than thorax; color pattern faint. Mouthparts of the herbivorous/detritivorous type [Type I (Stewart and Stark 1988)]. Labrum and clypeus with numerous long setae. Mandible typical for Leuctridae: 4 dorsal cusps (2 large, 2 small), and 1 small ventral cusp on side of first large dorsal cusp; bowl-shaped molar region, with transverse ridges in the "bowl," and with a pectinate scraping ridge on the ventromedial edge. Maxillary palpi 5-segmented. Labial palpi 3-segmented; glossae and paraglossae short and subequal in size (paraglossae slightly larger). Pronotum quadrangular; transverse anterior and posterior sclerotized bands; median longitudinal suture unsclerotized; color pattern weak. Mesonotum with two sclerites; anterior sclerite transverse and roughly trapezoidal; posterior sclerite roughly U-shaped. Metanotum like mesonotum. Wing pads three or more times as long as wide; posterior wing pads a little shorter than anterior wing pads; longitudinal axes of wing pads almost parallel to axis of body. Prosternum naked and membranous except for two small sclerites between the coxae; sclerites forming a posteriorly directed U-shape. Mesosternum narrowest anteriorly, widest by coxae; membranous except for weak sclerotization of the furcal pits and the Y-ridge; Y-ridge with faintly sclerotized double stem, arms connecting to posterior ends of furcal pits; transverse ridge connecting anterior ends of furcal pits. Metasternum similar to mesosternum; sclerotization only in a transversely rectangular area limited by the furcal pits, a transverse ridge connecting the anterior ends of the furcal pits, and the area between the pits and the ridge. All legs similar but increasing in size posteriorly; setation consists of abundant very small setae ("clothing hairs") and sparse longer setae; tibiae and femora with setal fringes; apex of tibiae with a pair of spines; tarsi 3-segmented, first segment short and conical, second very short, ringlike with apex cleft, third elongate and cylindrical, suture between first and second tarsomeres very narrow and hard to see; tarsomeres with ventral pad of numerous fine setae; tarsal claws slender. Abdominal terga very weakly sclerotized; setation sparse except on end of tenth segment. Abdominal fold present on segments I–VII. Subanal lobes incompletely fused. Cercal segments with apical fringe of 10–15 setae; setae about one-half length of the segments.



Figs. 4–7. *Calileuctra ephemera*: 4, male terminalia, dorsal view; 5, male terminalia, lateral view; 6, male terminalia, ventral view; 7, female terminalia, ventral view.





Figs. 8, 9. *Calileuctra ephemera*: 8, male subanal probe, right lateral view; 9, male subanal probe, ventral view.

EGG.—Shape oval; size uniform, 0.133 mm in length, 0.095 mm in width. Surface coarsely rugose; large, coarse punctures present in an irregular distribution.

TYPE LOCALITY.—CALIFORNIA: Napa Co., 3.36 km (2.1 mi) N on Hwy 128 from the intersection of Hwy 128 and Hwy 121, unnamed tributary to Capell Creek (ca 300 m [275 ft] elevation).

This intermittent stream has water present only a few months each year; some years there is no water (i.e., 1987 and 1990). When water is present, it flows down a small, steep canyon, across a grassy flat, under Hwy 128, and down a short cliff into Capell Creek. The stream course appears to be less than 350 m (1000 ft) long. All specimens have been collected in the grassy flat or just downstream. The stream course has a substrate of either bedrock or rocks on a clay soil. There is no obvious hyporheic zone. Detrital input is usually leaves from trees (mainly live oak), grass, and star-thistle.

TYPE SPECIMENS.—HOLOTYPE: male, type locality, 19 II 1983, WDS-A-160, reared from nymph. To be deposited in the entomology collection at the California Academy of Sciences, San Francisco, CA. ALLOTYPE: female, type locality, 25 II 1984, WDS-A-240. To be deposited with the holotype. PARATYPES: 1 male, type locality, 18 II 1984, WDS-A-234, reared from nymph (deposited at Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT); 3 females, type locality, 18 II 1984, WDS-A-234 (deposited with male paratype). Additional specimen: 1 nymph, type locality, 27 II 1988, WDS-A-527 (deposited with the holotype and allotype).

ETYMOLOGY.—The trivial name was selected to indicate the temporary nature of the stream at the type locality, and also to indicate the difficulty encountered when trying to collect specimens.

BIOLOGY.—All specimens were collected during the last two weeks of February, when the stream was flowing. Streams in this area of the coastal mountains experience a Mediterranean climate with a December-to-February rainy season. Local intermittent streams usually have surface flow only from January through March.

When first collected, all specimens were either late-instar nymphs (3) or adults (4). All field-collected adults (4 females) were swept from vegetation overhanging the stream. Two of the three nymphs collected were held in styrofoam containers until they molted to the adult stage. Both individuals were males.

The bowl-shaped molar region of the mandibles is similar to molar modifications found in beetle larvae that feed on fungal tissues, in general, and fungal spores, in particular (Lawrence 1977, Lawrence and Hlavac 1979, Lawrence and Newton 1980). Since fungal tissues are high in protein (Martin 1987), use of them as a food would aid the fast growth and development of nymphs.

Present information suggests that *Calileuctra ephemera* has a facultatively long egg diapause, very fast nymphal development, and short stadium for both nymphs and adults. The high protein content of fungal tissues (Martin 1987) may aid in the fast growth and development of nymphs of this unique species. These characteristics are similar to those of *Zealeuctra* (Snellen and Stewart 1979), an eastern North American genus and another inhabitant of intermittent streams.

Calileuctra dobryi, new species

Figs. 10–14

MALE.—General color brown; dark pattern as illustrated (Fig. 10). Length of body 4.0–6.0 mm. Macropterous, length of forewing 4.5–5.5 mm, wings light brown, venation similar to the genus *Perlomyia*. Tergum IX with membranous median band dividing tergum into two sclerotized halves, each half bearing a small, nipplelike projection and a large, earlike posterior projection. Tergum X also divided into two halves, each half with a gently rounded, knoblike lobe and an enlarged, lateral posterior lobe which ends in a sclerotized prong that extends about one-third the way up the cercus (Figs. 11, 12). Sternum IX broadly rounded posteriorly, extending only to base of subanal probe, large vesicle present at median anterior margin, vesicle with truncate apex (Fig. 13). Cerci enlarged, elongate, extending beyond genitalia posteriorly, sclerotized on lateral margins, apex rounded, ending in a sclerotized lateral prong (Figs. 11, 12, 13). Epiproct with narrow bifurcate apex (Fig. 11). Subanal probe large, elongate, broadest medially, apex pointed (Fig. 13).

FEMALE.—General color and wing venation similar to male. Length of body 5.0–6.0 mm. Macropterous, length of forewing 5.0–6.0 mm. Abdominal sternum VII enlarged, expanded slightly over VIII; posteromedial area formed into a narrow, medially rounded lobe. Sternum VIII small and only lightly sclerotized (Fig. 14).

NYMPH.—Unknown.

EGG.—Unknown.

TYPE LOCALITY.—CALIFORNIA: Los Angeles Co., South Fork Elsmere Canyon, San Gabriel Mountains. The type locality is a very small headwater tributary of Elsmere Creek. It has an extremely steep gradient and is hard to access. Thus, the habitat has been preserved more than the surrounding drainage area.

TYPE SPECIMENS.—HOLOTYPE: male, type locality, 22 IV 1991, K. F. Dobry. To be deposited in the entomology collection at the California Academy of Sciences, San Francisco, CA. ALLOTYPE: female, same data as holotype. To be deposited with holotype. PARATYPES: 1 male and 1 female, same data as holotype; 2 males and 1 female, CA: Los Angeles Co., Santa Monica Mountains, East Fork Arroyo Sequit, 5 mi NW Pacific Coast Highway off Mulholland Highway, 28 II 1992, K. F. Dobry; 2 females, CA: Orange Co., Santa Ana Mountains, Trabuco Canyon, 1300′, 11 I 1988, R. W. Baumann, B. J. Sargent, B. C. Kondratieff, and C. R. Nelson; 3 males and 1 female, CA: Los Angeles Co., San Gabriel Canyon, 23 IV 1960, D. Gibbo (LACM). Remaining paratypes to be deposited at Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT.

ETYMOLOGY.—The trivial name honors Keith F. Dobry, Los Angeles, CA, who collected many of the specimens.

BIOLOGY.—Specimens were collected as adults between January and April. All populations are from the Los Angeles basin and experience a Mediterranean climate.

PHYLOGENY

Leuctrid phylogeny has been examined from a cladistic point of view only two times. The two studies (Ricker and Ross 1969, Nelson and Hanson 1973) are somewhat contradictory. However, examination of the analysis given in both studies shows *Calileuctra* to possess many character states that are termed primitive or ancestral. Following Nelson and Hanson's more comprehensive analysis, the character states present in *Calileuctra* are as follows: 1-0, 2-0, 3-0, 4-0, 5-0, 6-0, 7-1, 8-0, 9-0, 10-2, 11-0, 12-0, 13-0, 14-2, 15-0, 16-0, 17-0, 18-0,19-0, 20-0, 21-1, 22-0, 23-0, 24-1, 25-1, 26-1, 27-1, 28-1, 29-0, 30-1, and 31-2 (first number = character; second number = character state). See Nelson and Hanson (1973) for a key to the characters and character states. Character states for *Calileuctra* and those cited in Nelson and Hanson (1973) for other leuctrid genera were run through the PAUP 3.1.1 program

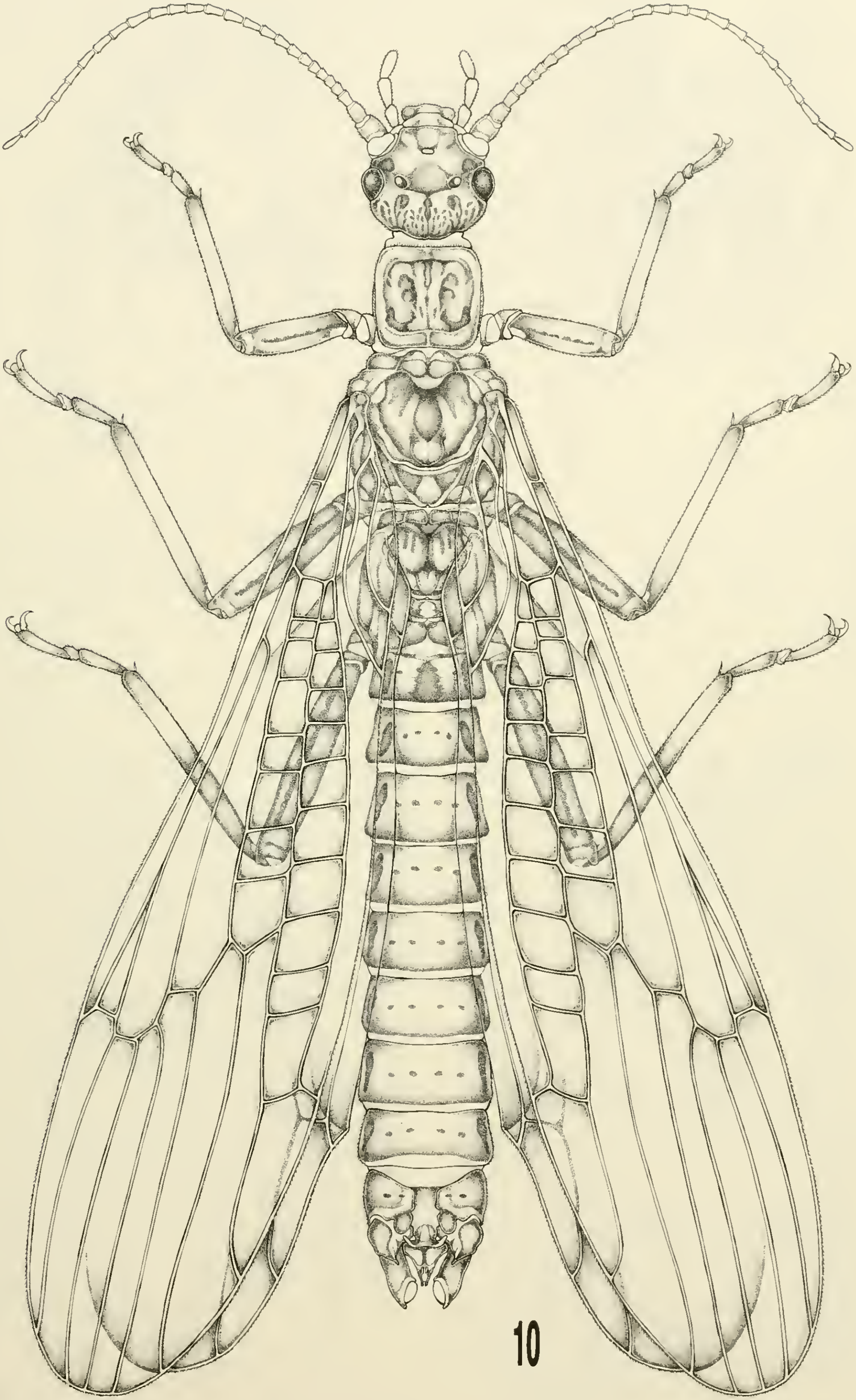


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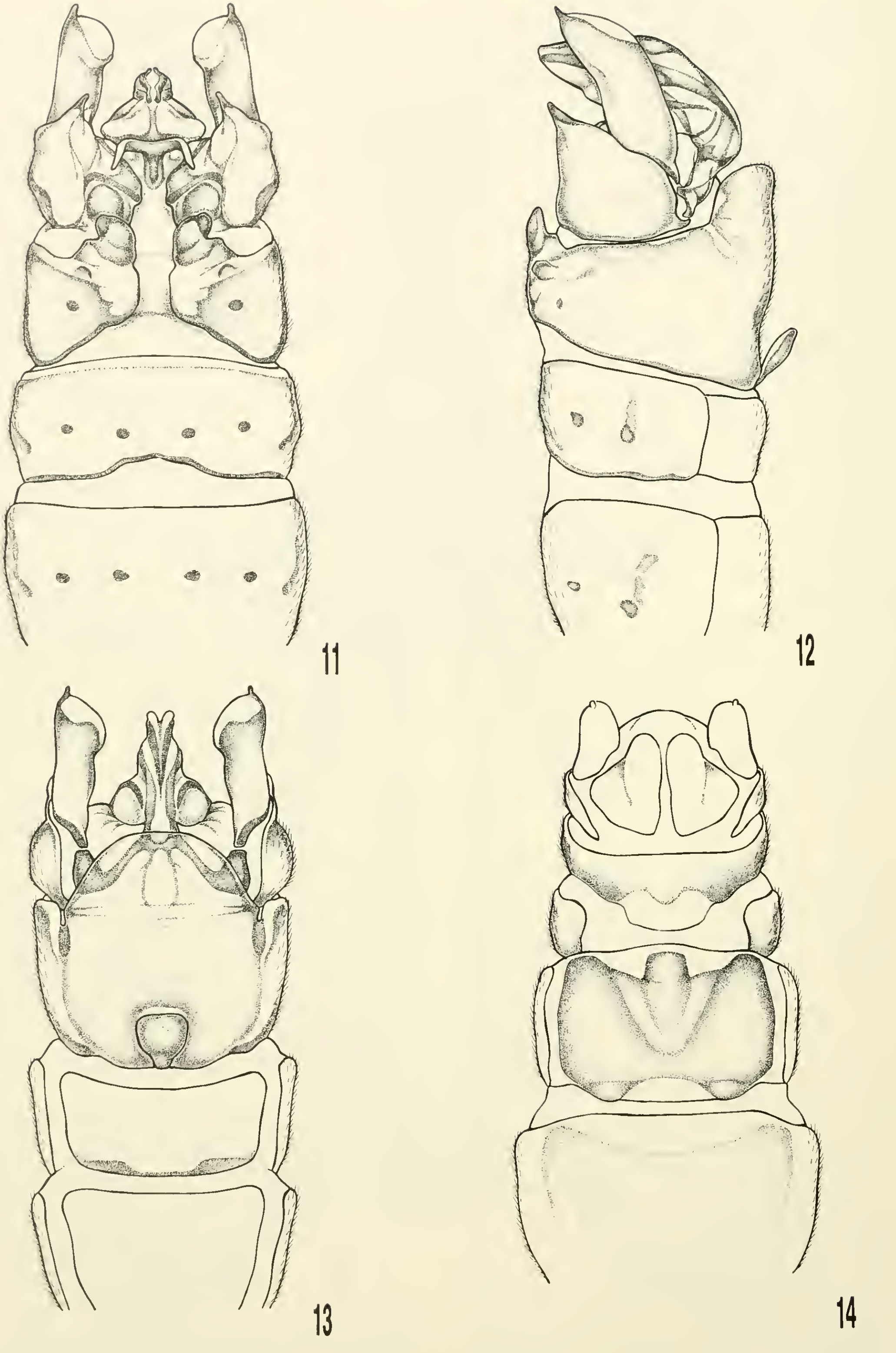
Fig. 10. *Calileuctra dobryi.* Habitus.



Figs. 11–14. *Calileuctra dobryi*: 11, male terminalia, dorsal view; 12, male terminalia, lateral view; 13, male terminalia, ventral view; 15, female terminalia, ventral view.

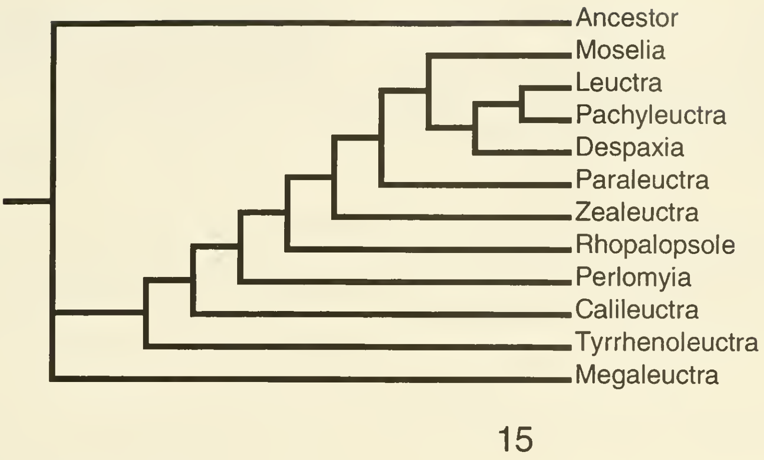


Fig. 15. Phylogeny of the Leuctridae.

using the branch and bound algorithm with all characters unordered. This analysis found one minimum-length tree (Fig. 15) with a length of 68, a consistency index of 0.82, and a retention index of 0.80.

This new tree is not considerably different from that given by Nelson and Hanson (1973). It differs only in the collapse of the sister group relationship between *Rhopalopsole* and *Zealeuctra* and the exclusion of *Euleuctra* and "*Leuctra*" *divisa* from consideration. The stability of this tree with *Calileuctra* added is taken as evidence of the consistency of this data set and the overall stability of this new classification. It is heartening to find the cladogram of Nelson and Hanson (1973) stable despite the previous "extinction" (i.e., absence) of *Calileuctra.* In this particular case, an "extinct" taxon did not particularly influence the overall topology of the cladogram. Hence, there is hope in our search for relationships among living taxa despite "known" extinction events.

In this tree, *Calileuctra* is a the sister-taxon of the group containing *Perlomyia, Rhopalopsole, Zealeuctra, Paraleuctra, Despaxia, Pachyleuctra, Leuctra,* and *Moselia.* In leuctrid phylogeny, *Calileuctra* occupies a near basal position and as such gives an important addition to our knowledge of the group.

ACKNOWLEDGMENTS

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CARBON ISOTOPE DISCRIMINATION IN THE C_4 SHRUB *ATRIPLEX CONFERTIFOLIA* ALONG A SALINITY GRADIENT

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ABSTRACT—Carbon isotope discrimination (Δ) was measured for leaves of *Atriplex confertifolia* along a salinity gradient in northern Utah. Over this gradient, the variation of Δ values was high for a C_4 species, and the Δ values were positively correlated with salinity in both years of the study. Of the possible explanations for this pattern, the Δ results are consistent with the notion that salinity induces an increase in the bundle sheath leakiness of these C_4 plants.

Key words: carbon isotope ratio, salt stress, bundle sheath leakiness, halophyte, desert ecology.

The analysis of carbon isotope ratios ($^{13}C/^{12}C$) has become a useful tool for understanding various integrated aspects of plant metabolism, including numerous investigations of plant-environment interactions. The impact of environmental factors on carbon isotope discrimination (Δ) by plants with C_3 photosynthesis has been well studied; however, only a limited number of studies have examined variation of Δ values in C_4 plants (O'Leary 1988, Farquhar et al. 1989, Peisker and Henderson 1992). In part, this disparity stems from C_4 plants having much smaller variation of Δ values than C_3 plants. Additionally, Δ values in C_3 plants have been correlated with water-use efficiency, and this has lead to an emphasis on applying carbon isotope analyses to breeding programs (Farquhar et al. 1989, Ehleringer et al. 1993). However, a few recent studies have demonstrated that variation of Δ values in C_4 plants may reflect environmental influences on physiological function (Bowman et al. 1989, Meinzer et al. 1994). In this study we examined variation of Δ values in a C_4 perennial shrub, *Atriplex confertifolia* (Torr. & Frem.) Wats., and its relationship to natural conditions of soil salinity.

The Δ value of a C_4 plant integrates two factors that can impact productivity: (1) the ratio of intercellular to ambient CO_2 concentration (c_i/c_a), which can reduce photosynthetic activity when low, and (2) bundle sheath leakiness (ø), which reduces photosynthetic efficiency when high. Farquhar (1983) modeled the relationship between these factors and carbon isotope discrimination in C_4 plants as

$$\Delta = a + (b_4 + b_3\text{ø} - a)\, c_i/c_a, \qquad (1)$$

where a (4.4‰) is discrimination against the heavier $^{13}CO_2$ molecule relative to the lighter $^{12}CO_2$ based on differential rates of diffusion, b_3 (29‰) is the discrimination due to a greater affinity for $^{12}CO_2$ relative to $^{13}CO_2$ by ribulose bisphosphate carboxylase (Rubisco), and b_4 (typically ≈ –5.2‰) is discrimination based on the steps leading to, and including, CO_2 fixation by phosphoenol pyruvate carboxylase (PEPC) after atmospheric CO_2 enters the leaf. The b_4 term varies slightly as a function of temperature and is negative (greater proportion of $^{13}CO_2$) due to fractionation associated with the hydration of CO_2 to HCO_3^- (Mook et al. 1974). The discrimination terms of Equation 1 (a, b_3, and b_4) are constants, for the most part, and thus differences among Δ values are the result of changes in ø and/or c_i/c_a during CO_2 assimilation.

In C_4 plants, CO_2 is initially fixed by PEPC in the mesophyll cells, transported and decarboxylated in the bundle sheath cells, and then refixed by Rubisco. However, before the assimilation by Rubisco a fraction of the CO_2 may diffuse out through apoplastic portions of the bundle sheath cells. This is known as "leakiness" and is thought to be reduced by suberization of bundle sheath surfaces (Farquhar 1983). This leakiness, however, may be increased by environmental stresses, such as salinity (Bowman et al. 1989), and an increase

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in leakiness represents an energetic cost to the plant as a result of incomplete carbon assimilation or overcycling (Ehleringer and Pearcy 1983, Jenkins et al. 1989, Henderson et al. 1992).

Leakiness affects Δ because it causes the bundle sheath cell to become an open system and therefore allows expression of discrimination by Rubisco (b_3). The proportion of CO_2 that leaks out of the bundle sheath cell (ø) modifies the degree to which b_3 is expressed and thereby determines the relationship between Δ and c_i/c_a (Eq. 1). At low ø values the relationship between Δ and c_i/c_a is negative, at high ø the relationship is positive, and at $ø \approx 0.32$, Δ is constant at 4.4‰ regardless of c_i/c_a. Equation 1 also predicts that for any given c_i/c_a, an increase in ø results in an increase in Δ. Given these relationships, variation of Δ values in C_4 plants can provide an indication of bundle sheath leakiness and its relationship to environmental stresses.

To date, much work investigating variation of Δ in C_4 plants has come from either laboratory gas exchange studies (Evans et al. 1986, Bowman et al. 1989, Henderson et al. 1992) or theoretical models (Peisker 1982, Farquhar 1983, Peisker and Henderson 1992). There is little direct information on environmental stresses that influence Δ in natural populations of C_4 plants (except see Walker and Sinclair 1992). Here we report on changes in Δ values for the C_4 species *Atriplex confertifolia* found along a natural salinity gradient in Utah. The purpose of this study was to determine if Δ values changed in relation to soil salinity under field conditions, and if these changes corresponded to variation in ø values. Two previous laboratory studies have shown that higher soil salinity does increase Δ values in C_4 plants and that this change is a result of greater ø (Bowman et al. 1989, Meinzer et al. 1994). For *A. confertifolia*, we hypothesized that the same trend would be found over a transect of naturally increasing soil salinity.

METHODS

Study Sites

Four study sites of increasing salinity were chosen along a south-to-north transect in the northern end of Skull Valley (Tooele County, UT) flanking the western slope of the Stansbury Mountain Range. The four sites range in elevation from 1366 m to 1286 m (Fig. 1). Site 1 (1366 m) is dominated by sagebrush (*Artemisia tridentata*) with low densities of *Atriplex confertifolia*, *Juniperus osteosperma*, and *Tetradymia spinosa*. Weedy grasses and annual species of the Chenopodiaceae are also found within disturbed areas of this and all other sites. Greasewood (*Sarcobatus vermiculatus*) is the dominant species at sites 2 (1317 m) and 3 (1294 m) with *A. confertifolia* co-occurring in low frequency. Site 4 (1286 m), along the margins of the salt flats, is a heterogeneous site with a mixed community of salt-tolerant species. *S. vermiculatus* is the dominant species with moderate densities of *Allenrolfea occidentalis*, *Atriplex gardneri*, *A. confertifolia*, *Chrysothamnus viscidiflorus*, *Kochia americana*, and *Suaeda torreyana*.

Weather data for this transect are taken from the Grantsville weather station (Grantsville, Tooele County, UT, 1307 m) located 17.3 km E and 8.2 km S from the center of our study transect.

Leaf and Soil Samples

Leaves of *Atriplex confertifolia* and soil samples were collected from each of the four transect sites in October 1991 and 1992, with the help of the 1991 and 1992 Plant Ecology classes from the University of Utah. Recently matured leaves of *A. confertifolia* were collected from five to eight individuals per site in 1991 and three per site in 1992. Leaf samples were oven-dried (70°C, 7 d), ground with mortar and pestle, and analyzed for carbon isotopic composition (Windy Ike, Delta S mass ratio spectrometer, Finnigan-MAT, San Jose, CA) relative to the Pee Dee Belemnite standard. Analyses were done at the Stable Isotope Ratio Facility for Environmental Research (SIRFER, University of Utah, Salt Lake City, UT). Carbon isotope ratio values (δ) were transformed to discrimination (Δ) values as

$$\Delta = (\delta_a - \delta_p)/(1 + \delta_p), \qquad (2)$$

where δ_p is the measured carbon isotope ratio of the plant, and δ_a is the carbon isotope ratio of CO_2 in the atmosphere (−.008 or −8‰; Farquhar et al. 1989). The standard per mil (‰) notation is used throughout for ease of presentation, and the overall, long-term error

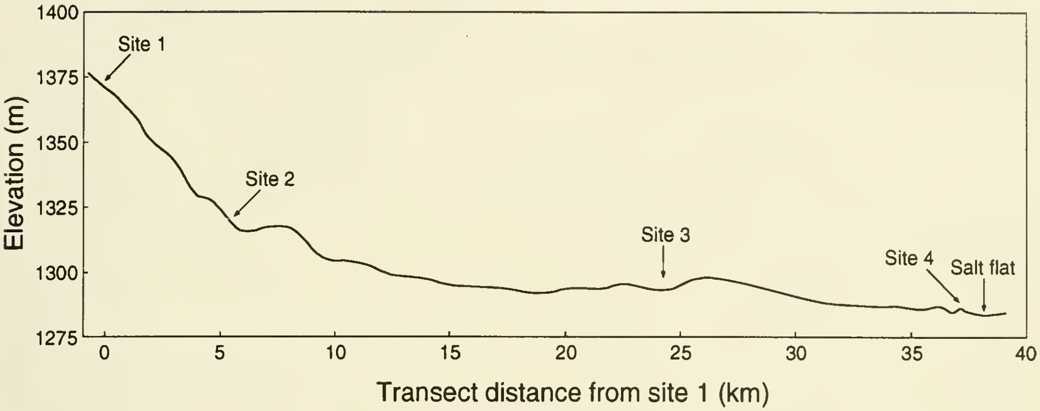

Fig. 1. Study transect in cross section. Shown is the topography over the transect and localities of each study site based on the approximate linear distance from site 1.

associated with carbon isotope determination is ± 0.11‰.

Soil samples were collected from two depths (15–20 cm and 40–60 cm) in two to six excavation pits at each site. Approximately 200 g of freshly extracted soil from each hole and depth was placed immediately into soil canisters, sealed, and kept cool until analysis in the laboratory. In the lab one subsample per canister was removed for salinity analyses. The remaining soil was used for gravimetric water content determination based on the difference between soil fresh (wet) weight and dry weight (i.e., water content) relative to the soil dry weight. Soils were dried at 70°C for 7 d.

In 1991 the soil salinity analysis was based on electrical conductivity (EC) of an aqueous solution extracted from a 1:2 soil:deionized water mixture, and in 1992 from a 1:5 soil: deionized water mixture. There was no evidence that the 1:2 mixture was ion saturated; thus, to standardize these ratios, the ECs of samples using a 1:2 solution were extrapolated to EC based on a 1:5 ratio assuming a linear dilution relationship. Tests confirmed that this extrapolation was valid even for EC values higher than those found in actual field samples.

Although a more standard procedure for salinity determination is the "soil paste" method, the 1:5 ratio method we used is recommended as a simpler technique to determine relative salinity contents (Rhoades 1982) and is suitable for the purposes of this study (i.e., standardized comparison of relative salinities among sites). Additionally, the ECs of 1:5 ratio extracts are highly correlated with soil paste ECs for soils within and near our transect (D. G. Williams unpublished data). Electrical conductivity is reported in μmhos cm^{-1} (1 μmhos cm^{-1} = 0.1 mS m^{-1} = 0.502 mM NaCl), and the data were log transformed for statistical analyses. Interannual comparisons of means for each soil trait were done by *t* tests, and correlations between soil trait and plant carbon isotope discrimination means were determined by Pearson product-moment correlation.

RESULTS

Transect Characterization

Salinity increased across the gradient in both the 1991 and 1992 samples; electrical conductivity increased by two orders of magnitude over the entire transect (Table 1). Site 1 was the least saline, and salinity progressively increased toward the highly saline site 4.

There were few differences between years in soil electrical conductivity. Significant differences were found at only two sites and at only one depth per site. Furthermore, sites gave opposite results: soils of site 3 at the 15–20-cm depth had greater conductivity in 1991 than 1992 ($t = 4.33$, $P < .01$), and soils from site 1 at the 40–60-cm depth had higher conductivity in 1992 than in 1991 ($t = 4.60$, $P < .01$).

Gravimetric water content also increased over the transect from site 1 to site 4 (Table 1). Soil water content was somewhat greater in

TABLE 1. Soil properties at two depths for sites 1–4 along the study transect (n = number of pits; one sample for each depth per pit). Soil water content was measured as gravimetric water content, and electrical conductivity is of an aqueous extract from 1:5 soil:water mixture (extrapolated for 1991 from 1:2 ratio; see text).

	Soil water content (%) @15-20 cm			Soil water content (%) @40-60 cm			Electrical conductivity (μmhos/cm) @15-20 cm			Electrical conductivity (μmhos/cm) @40-60 cm		
	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*
OCTOBER 1991												
Site 1	4.66	0.300	4	5.34	0.234	4	89	15.7	4	70	3.2	4
Site 2	4.15	0.687	4	7.23	0.360	4	91	7.6	4	324	81.1	4
Site 3	11.79	1.446	4	17.24	0.892	4	2309	114.1	4	2066	657.7	4
Site 4	24.84	7.578	6	39.41	7.841	6	3596	587.6	6	3382	530.7	6
OCTOBER 1992												
Site 1	2.89	0.454	2	3.81	0.402	3	84	6.3	3	93	3.7	3
Site 2	4.79	0.226	2	5.56	0.499	3	144	29.2	3	324	111.0	3
Site 3	2.46	0.270	2	10.26	3.672	3	546	459.3	3	984	858.5	3
Site 4	10.66	0.950	2	NA	—	—	1640	1440.0	2	3250	350.0	2

1991 than in 1992, but significant differences at both depths were found only at site 1 (15–20-cm depth, $t = 3.34$, $P < .05$; 40–60-cm depth, $t = 3.52$, $P < .05$). Rainfall over the 10-wk period prior to sampling in 1991 was much greater than that of 1992 (82.5 mm vs. 18.8 mm), which likely accounts for the trend of greater water content in the soils during the 1991 sample period.

Carbon Isotope Discrimination

Along the transect the carbon isotope discrimination for *Atriplex confertifolia* ranged from a low of 4.74 ± 0.96‰ at site 1 in 1992, to a high of 6.55 ± 0.11‰ at site 3 in 1991 (Fig. 2). This range of nearly 2‰ is high for C_4 plants (Farquhar et al. 1989). The mean Δ value was always greater than 4.4‰, and for only a single sample was the individual shrub value less than 4.4‰. These high Δ values indicate that the mean ϕ values were always greater than 0.32 (Eq. 1).

With respect to the environmental parameters examined along the transect, mean leaf Δ was not significantly correlated with water content during any observation, but was positively correlated with log EC (Fig. 2). Inclusion of the notably low Δ value of site 4 in 1991 resulted in a nonsignificant, positive trend (but when excluded, Δ was significantly correlated with log EC in 1991 at the deeper soil depth, $R = 1.0$, $P < .01$). In 1992 there was a highly significant, positive correlation of Δ and log EC for both the shallow soils ($R = .978$, $P < .05$) and deeper soil depths ($R = .999$, $P < .001$) (Fig. 2).

DISCUSSION

Variation in carbon isotope discrimination values of C_4 plants is, in part, dependent upon the proportion of CO_2 that is initially fixed by PEPC and ultimately diffuses out of the bundle sheath cells without being refixed (i.e., the leakiness, ϕ). Leakiness might be influenced by environmental stresses, such as salinity (Bowman et al. 1989, Meinzer et al. 1994), because such stresses could disrupt membrane properties or the biochemical coordination between the C_4 and C_3 cycles operating in the mesophyll and bundle sheath cells, respectively (Peisker and Henderson 1992). The other component influencing variation of Δ in C_4 plants is c_i/c_a. Figure 3 illustrates how the relationship between Δ and c_i/c_a depends upon the value of ϕ (from Eq. 1), and provides a model for how changes in ϕ and c_i/c_a can account for the changes in Δ values we observed.

We found that Δ values of *A. confertifolia* increased by 2‰ in concordance with increasing salinity (Fig 2). These Δ values were always greater than 4.4‰; therefore the ϕ values must be greater than 0.32 (cf. Fig. 3). A 2‰ increase in Δ values, at $\phi > 0.32$, cannot be explained solely by changes in c_i/c_a given the typical range of c_i/c_a values for C_4 plants under ambient conditions (0.20–0.40; Pearcy and Ehleringer 1984). To do so would require either extreme leakiness values ($\phi \geq 0.6$) or an increase of c_i/c_a with increasing salinity since Δ and c_i/c_a are positively related when $\phi >$ 0.32. Leakiness values greater than 0.6 have

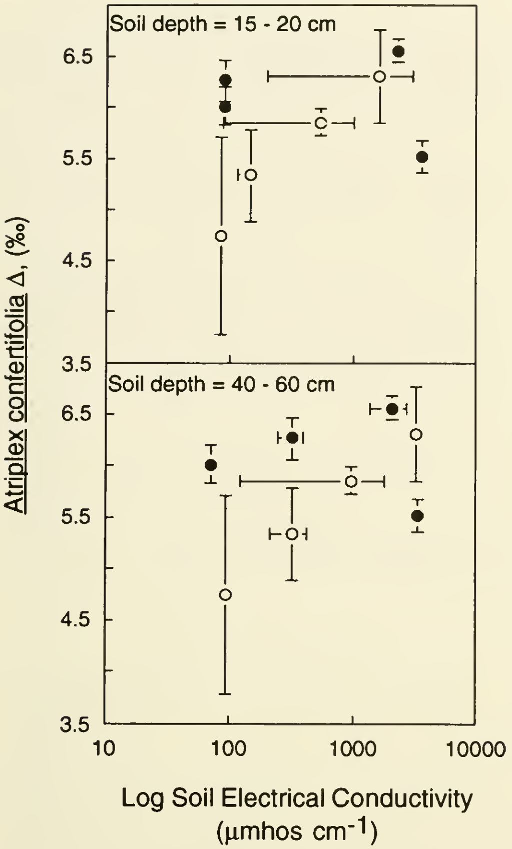

Fig. 2. Relationship between carbon isotope discrimination (Δ) of *Atriplex confertifolia* leaves and log electrical conductivity (log EC) of soil at two depths, 15–20 cm and 40–60 cm, for sites 1–4 along the transect. Closed symbols (●) are study site means for 1991, and open symbols (○) are those for 1992. Error bars are ± 1SE.

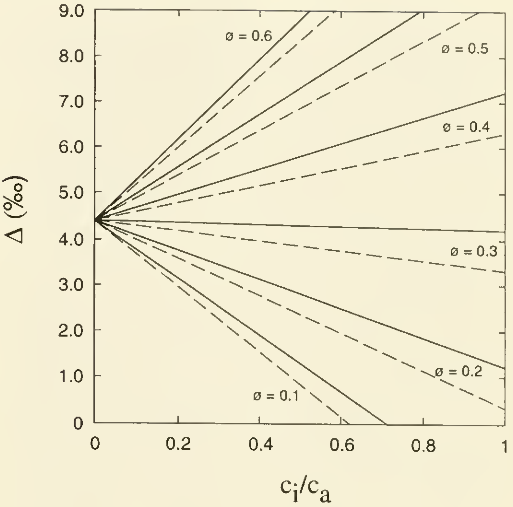

Fig. 3. Model for the relationship between carbon isotope discrimination (Δ) and c_i/c_a (ratio of intercellular to ambient CO_2) based on Equation 1 and for ø values ranging from 0.1 to 0.6. Dashed and solid lines represent the range of Δ values for each ø value depicted, based on a high leaf temperature (34°C) where $b_4 = -4.8‰$ (solid line) and a lower leaf temperature (25°C) where $b_4 = -5.7‰$ (dashed line).

never been reported, and the latter explanation is unlikely since salt stress typically decreases or does not change c_i/c_a (Long and Baker 1986, Flanagan and Jefferies 1988). A simpler explanation for the change in Δ values is that ø increases with higher salinity. A 2‰ increase based on changes in ø values can be easily accommodated within the limits of c_i/c_a found for C_4 plants (Fig. 3). Thus, changes in Δ values for *A. confertifolia* are more likely due to an increase of ø associated with a change in salinity; consequently, the presence of a significant relationship between Δ values and EC (Fig. 2).

The trend of increasing Δ values with increasing salinity held in all but one site in the two-year study (site 4 in 1991). This deviation could be due simply to the high degree of edaphic variability at site 4; this location had the greatest topographic variability, highest species diversity, and greatest overall variance for soil conductivity and water content (Table 1). Site 4 was also extremely wet in 1991 (near 40% water content at 40–60-cm depth), which may have diluted the salinity of these soils, thereby reducing the salinity experienced by the plants. Without a more detailed study, however, this deviation remains unexplained.

Previous studies have found contrasting patterns of the relationship between Δ and salinity. In a laboratory study with 11 C_4 species, Henderson et al. (1992) found that ø values were invariable and low, remaining at ø ~0.21, thereby resulting in a negative relationship between Δ and c_i/c_a (Fig. 3). The small variation they observed in Δ values was attributed to changes in c_i/c_a values. However, in an earlier study with the C_4 monocots *Zea mays* and *Andropogon glomeratus*, Bowman et al. (1989) found that Δ values of salt-stressed plants were more dramatically influenced by changes in c_i/c_a than were control plants. The increase of Δ values with salinity was explained by a changing relationship between Δ and c_i/c_a due to increasing ø values as the water status of salt-stressed plants declined through the day (Bowman et al. 1989).

Recently, Meinzer et al. (1994) also observed that increasing salinity resulted in increases of Δ values. Using two sugarcane cultivars, they showed that change in Δ value could be ascribed to greater ø values as salinity increased, and that variability of c_i/c_a had much less impact on the increase of Δ values. In contrast, Walker and Sinclair (1992) reported that Δ values of two Australian C_4 *Atriplex* species *decreased* at sites with increased salinity. The Δ values of these Australian *Atriplex* leaves were greater than 4.4‰, which could have been achieved only with a bundle sheath leakage greater than 0.32 (Fig. 3). Since the relationship between Δ and c_i/c_a is positive at $ø > 0.32$ (Fig. 3), the Walker and Sinclair data suggest that salinity affected a decrease of c_i/c_a and, therefore, a decrease of Δ.

Our findings of a positive correlation between Δ values of *Atriplex confertifolia* and salinity are in contrast to findings of Walker and Sinclair (1992). Our observations, like those of Bowman et al. (1989) and Meinzer et al. (1994), suggest that changes in leaf carbon isotope discrimination result from an increased bundle sheath leakage when plants are exposed to a salinity stress. The mechanism of change in ø values is likely to be associated with physical changes in the bundle sheath permeability to CO_2 (or to HCO_3^-) and/or biochemical changes in the coupling of Rubisco and PEPC activity. Such biochemical changes due to salinity have been previously found. Guy and Reid (1986) have shown that salinity may reduce Rubisco activity in C_3 plants without a concomitant decrease in PEPC activity. Increased salinity (NaCl) has also been shown to increase PEPC activity in some C_4 halophytes (Shomer-Ilan et al. 1985). Any such increase in the activities of C_4 carboxylation enzymes relative to those of C_3 carboxylation enzymes in C_4 plants should increase ø values (Peisker and Henderson 1992). Thus, under natural conditions it appears that salinity could increase Δ values of *A. confertifolia* by influencing an increase in ø values.

The relationship between salt stress and ø of C_4 plants may be species specific or even population specific and may account for discrepancies among different studies of Δ values in C_4 plants. For example, there is high variability among previous studies of carbon isotope discrimination in *Atriplex confertifolia*; mean Δ values range from 4.4‰ (Marino et al. 1992) to 6.9‰ (Troughton et al. 1974). Yet, each of these observations is consistent with the notion that ø values exceed 0.32 and are therefore high compared to nonhalophytic C_4 species (Henderson et al. 1992).

In the present study we have shown that salinity may be one factor that significantly influences variation of Δ values in C_4 plants, most likely through an effect on bundle sheath leakiness. While variation in Δ values of C_4 plants may provide new insights into plant-salinity dynamics along environmental gradients, results also suggest that caution is necessary when using Δ values of C_4 plants to interpret historical changes in atmospheric CO_2 concentrations and ^{13}C values, as has been proposed by Marino et al. (1992).

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DEMOGRAPHY OF *ASTRAGALUS SCAPHOIDES* AND EFFECTS OF HERBIVORY ON POPULATION GROWTH

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ABSTRACT.—Losses in fecundity due to predispersal herbivory can be large; however, the effects of this loss on long-term population viability have rarely been investigated. I conducted a demographic study of *Astragalus scaphoides* (Fabaceae), a long-lived perennial endemic to east central Idaho and adjacent Montana, by following mapped individuals at two sites from 1986 to 1993. *Astragalus scaphoides* suffers losses of predispersal fecundity averaging nearly 50% from insect seed predation and inflorescence predation by insects and livestock. Cattle reduced fecundity by 0–85%. Nonetheless, estimates from matrix projection models indicate that both sample populations had positive growth in most years. Elasticity analyses revealed that population growth occurred in spite of relatively small contributions by recruitment compared to growth and survival of nonreproductive plants. Results suggest that populations of this long-lived perennial depend little on reproduction and recruitment for growth and can persist in association with seasonal-rotation livestock grazing.

Key words: demography, herbivory, livestock grazing, predation, matrix projection models, elasticity analysis, Astragalus, *rare plant.*

The importance of herbivory in determining plant population dynamics and composition of vegetation has long been debated (Ehrlich and Birch 1967, Slobodkin et al. 1967, Belsky 1986). A great deal of evidence suggests a negative impact of herbivory on the host plant (Harper 1977, Crawley 1983, Dirzo 1984); however, researchers have recently presented evidence for positive interactions (McNaughton 1986, Paige and Whitham 1987).

A plant's life history plays an important role in determining the effects of herbivory. Loss of reproductive output from seed predators can be disastrous for an annual or biennial but may have little effect on a long-lived perennial. Furthermore, effects of herbivory will depend on the age or stage (e.g., seeds, adults) at which it occurs (Dirzo 1984). Most studies have focused on the effects of herbivores on particular components of fitness over relatively short time spans. This is unfortunate because it is the long-term effect on population growth that determines the importance of herbivory to population viability. Few studies have integrated the effects of herbivory on population dynamics and growth (Harper 1977; but see Louda 1982, 1983).

Predation, particularly by exotic species, has often been cited as a threat to endangered plant populations (Greig-Smith and Sagar 1981, Parsons and Browne 1982, Willoughby 1987, Norton 1991, Pavlik et al. 1993). Negative impacts of herbivores were shown, but a causal link to declining population size has rarely been demonstrated.

Astragalus scaphoides (Jones) Rydb. is endemic to a small area of east central Idaho and adjacent Montana (Barneby 1964). It was formerly a candidate for listing as a threatened or endangered species by the U.S. Fish and Wildlife Service (Category 3C; USDI–FWS 1993) and is currently listed as sensitive in Idaho (Moseley and Groves 1990) and Montana (Lesica and Shelly 1991). Most populations of *A. scaphoides* occur on public lands subject to livestock grazing. High levels of inflorescence and seed predation have been observed in some populations (Lesica and Elliott 1987a). Here I report the results of an eight-year demographic study of *A. scaphoides* at two sites. The purpose of the study is to document levels of herbivory and to assess its importance to population growth using stage-based transition matrix models and elasticity analysis (de Kroon et al. 1986, Caswell 1989).

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METHODS

Species Studied

Astragalus scaphoides is a caulescent perennial with a taproot surmounted by a branched caudex. Reproductive individuals are 20–50 cm high with a cluster of pinnately compound basal leaves and 3–10 leaves at intervals along the erect stem. The inflorescence is composed of 1–4 racemes arising from the axils of the upper leaves. Each raceme is composed of a naked peduncle, 5–15 cm long, surmounted by a tight cluster of 10–30 flowers that expands in fruit. Nonreproductive individuals generally have 1–4 basal leaves and may have a sterile stem less than 15 cm tall with 1–5 leaves. The branching caudices of reproductive plants may bear up to four stems and more than a dozen racemes (Barneby 1964, Lesica unpublished data).

Astragalus scaphoides generally flowers during the first three weeks of June. The most conspicuous form of herbivory of these plants is the removal of inflorescences during flowering. Inflorescence predation has two principal sources: insects and livestock. Ants (subfamily Formicinae) and moth larvae (*Melacosoma* spp., family Lasiocampidae) were observed removing inflorescences at a site near Haynes Creek in Idaho. Peduncles below the flowers were girdled, and withered inflorescences were often still present near the base of the plant. Inflorescence predation by livestock also occurred but differed from insect predation in that peduncles were all removed at the same height, and severed inflorescences were not found below the plants. In either case the cluster of basal leaves was usually left intact. It was possible to assign primary responsibility for inflorescence herbivory at a site in a particular year to either insects or ungulates based on the appearance of damaged plants and the presence or absence of droppings, hoof prints, or trampled vegetation. However, it was not possible to unambiguously assign each case of herbivory to one or the other source. Inflorescence predation by insects was observed at both study sites in all years that inflorescences were produced, but ungulate predation was common only at Sheep Corral Gulch.

Predispersal seed predation occurred at both sites in most years. Larvae were collected from developing legumes in 1986 and identified as weevils, small beetles in the family Curculionidae. Weevil larvae feed on maturing seeds and leave the developing or mature legume by creating a small hole in the outer wall. Seed predation by weevil larvae was inferred from the presence of fecula and/or an exit hole in the legume.

Study Sites

The Sheep Corral Gulch population occurs in southern Beaverhead County, MT, on a gentle south-facing slope at 1920 m (T8S R12W S16). Mean July and January temperatures at Dillon, 32 km NW and 275 m lower, are 19.0° and –6.6° C, respectively. Mean annual precipitation is 241 mm. Vegetation is dominated by *Artemisia tridentata* and *Agropyron spicatum*. *Aster scopulorum* and *Phlox hoodii* are common forbs. Livestock were managed on a rest-rotation system by which grazing occurred in different seasons in most consecutive years. Evidence of heavy spring grazing by livestock was observed in 1989, 1990, and 1993.

The Haynes Creek population is in central Lemhi County, ID, approximately 48 km W of Sheep Corral Gulch. It occurs on a moderate southeast-facing slope at 1555 m (T19N R23E S2). Mean July and January temperatures at Salmon, 24 km NW and 365 m lower, are 16.2° and –6.7° C, respectively. Mean annual precipitation is 252 mm. Vegetation is dominated by *Artemisia tridentata*, *Agropyron spicatum*, and *Bromus tectorum*. This site was not grazed by livestock before early July during the course of the study.

Field Methods

Two permanent monitoring transects were established at each of the study sites in early July 1986 following methods outlined in Lesica (1987). Transects were located subjectively to represent the populations and were read in early July because fruits were mature or nearly so, but seed dispersal had not yet begun. At each site the transects were parallel to each other and the slope. Each transect consisted of 50 adjacent 1-m^2 mapping quadrats placed along the transect line. The position of each *A. scaphoides* plant encountered in the quadrats was mapped and classified for three traits: (1) size, (2) inflorescence production, and (3) fecundity using the following classification:

(1) Size classes:
    D Dormant (no aboveground parts observed)
    S Small nonreproductives (1-3 leaves)
    L Large nonreproductives ($\geq$ 4 leaves)
    R Reproductive
(2) Inflorescence production:
    A Inflorescence produced no fruit
    P Inflorescence was removed due to predation
    I Inflorescence produced at least one mature fruit
(3) Fecundity: total number of mature fruits

When stems were removed below the point of inflorescence articulation, I made a conservative estimate of the number of inflorescences removed based on the size of the remaining plant. Evidence of livestock and native ungulates (e.g., droppings, hoof prints, trampled vegetation) was noted along each transect and for the site as a whole.

I found that some plants would go undetected for one to several years but reappear in subsequent years (Lesica and Steele 1994). These "dormant" plants may have produced small leaves that had senesced and disappeared by early July; however, my observations in May and June suggest that most of them produced no vegetation on the years in question. The presence of dormant plants can be inferred by comparing transect maps from the full sequence of years. The proportion of dormant plants ranged from 1% to 23%, with a mean of 10% in 1987–1991. Plants have "disappeared" for as many as five years before reappearing. However, in 1986–1992 at the two sites, 71% of dormant plants reappeared after one year, and 88% reappeared after two years (Lesica and Steele 1994). As a result, ca 10% of the plants were undetected in the first and last years of the study, and ca 3% were undetected in the second and second from last years. Thus, I have chosen to eliminate the first and last years (1986, 1993) of the study from demographic analysis, recognizing that a small (ca 3%) error still remains in mortality and recruitment estimates in 1987 and 1992.

On years when fruit production was adequate, I collected 50 randomly selected mature fruits from at least 25 plants. I opened the pods, counted intact seeds, and recorded evidence of insect predation.

Data Analysis

Stage-structured transition matrix projection models summarize the way in which survival, growth, and reproduction at various life-history stages interact to determine population growth (van Groenendael et al. 1988, Caswell 1989). Matrix projections assume fixed transition probabilities between stages in a population through time (Lefkovitch 1965, Menges 1990). They also assume density-independent population growth and thus do not give an accurate projection of long-term population future. Nonetheless, they can be used to summarize short-term population dynamics (Caswell 1989). One-year transition probabilities were estimated as the number of plants in life-stage class *i* moving into class *j* over the course of one year divided by the number of plants in stage *i* at the beginning of the year. This method assumes that an individual's transition depends only on its life-stage class at the beginning of the period and is independent of its transition the previous year. The equilibrium growth rate (λ) is the dominant eigenvalue of the transition matrix (Lefkovitch 1965, Caswell 1989). $\lambda > 1.0$ indicates population increase, while $\lambda < 1.0$ indicates decrease. λ integrates the effects of survival, growth, and fecundity of the different life-history stages into a single parameter. There are two ways in which a reproductive plant can undergo a transition: (1) the plant itself moves into a different class or stays the same and (2) the plant produces progeny in one or more classes. These two probabilities (Recruit, Repro) are presented separately in the matrices but must be added together to solve for λ. Details on the construction and use of matrix population models can be found in Caswell (1989) and Menges (1990). λ was calculated using RAMAS/stage (Ferson 1991).

Elasticity measures the relative change in the value of λ in response to changes in the value of a transition matrix element. Elasticity matrices allow comparison of the relative contributions of various life-history transitions to population growth and fitness (de Kroon et al. 1986). Elasticities sum to unity, and regions of the matrix may be summed to compare the importance of growth and survival to recruitment

(Caswell 1989). Elasticities for nonreproductive plants are sums from the small (S) and large (L) classes. Elasticities were calculated using RAMAS/stage (Ferson 1991).

When the majority of seeds pass directly from production to germination in less than one year, seeds should not appear as a separate stage in matrix models (Caswell 1989, Silvertown et al. 1993). Seeds of *Astragalus scaphoides* germinate readily without stratification (Lesica and Elliott 1987b), suggesting that most seeds germinate the same year they are produced. Nonetheless, *A. scaphoides* may form a seed bank. Not including a seed bank in the matrix model may affect the value of λ (Kalisz and McPeek 1992), especially when it is <1.0. However, it will have little effect on analyses based on elasticities (Silvertown et al. 1993). I calculated separate elasticities for reproductive transitions and recruitment by dividing the reproductive + recruitment elasticities proportionately between the two components.

Losses to predation were estimated from the number of inflorescences lost using the calculated means for seeds/fruit and fruits/inflorescence. Cumulative fecundity losses were calculated by multiplying the proportions of inflorescences and seeds remaining after predation and subtracting from one.

RESULTS

Population Growth

The number of *Astragalus scaphoides* plants in the transects at both sites increased by about one-third between 1986 and 1993 (Fig. 1). Equilibrium population growth rate (λ) was $\gtrsim 1.0$ at both sites over the course of the study and was >2.5 at Sheep Corral Gulch in 1988–89 and 1990–91. At no time during the study was $\lambda < 0.8$ at either site (Table 1).

Survivorship

Between 40% and 50% of the *Astragalus scaphoides* plants observed at the start of the study in 1986 were still alive in 1993 (Fig. 2). Approximately 50% of the 1989 cohort (the first large cohort recruited during the study) survived for more than 3–4 years. Taken together these results indicate that *A. scaphoides* is a long-lived perennial, with ca 50% mortality occurring in the first 3–4 years, but a large proportion of plants living to be ≥ 10 years.

Predation

Inflorescence predation attributable to ungulates was virtually absent from the Haynes Creek population. Droppings and hoof prints of cattle were the only signs of ungulates at Sheep Corral Gulch. Droppings occurred in 3–9% of the mapping quadrats during the study. Inflorescence predation by insects occurred at both sites in all years.

A significant number of inflorescences were produced in six of eight years at Haynes Creek, and inflorescence predation accounted for fecundity losses of 14–50% over the course of the study (Fig. 3). Most of this herbivory was attributable to insect damage. At Sheep Corral Gulch reproductive plants were common in only four of eight years. Inflorescence predation resulted in fecundity losses of 19–90%, and the proportion of inflorescences lost to predation was highest in 1989, 1990, and 1993, years in which predation was due mainly to livestock (Fig. 3).

Seed predation occurred at both sites in nearly every year in which significant fruiting occurred (Fig. 3). Overall, loss of seeds to weevil predation ranged from 0 to 33% with a mean of 18%. Insect seed predation was generally higher at Sheep Corral Gulch than at Haynes Creek (Fig. 3).

Losses of fecundity due to the combined effects of inflorescence and seed predation were 19–90% in 1986–1993, with means of

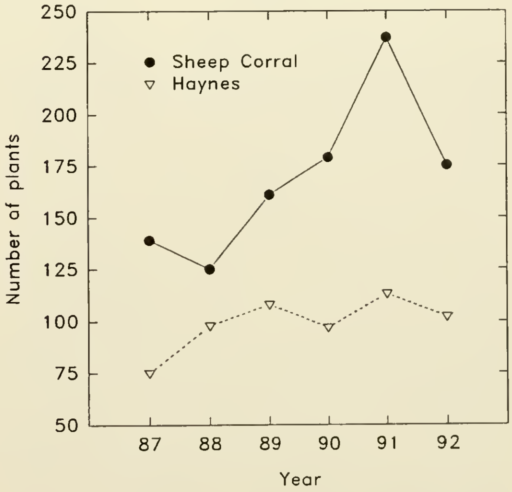

Fig. 1. Density of *Astragalus scaphoides* plants in the two sample populations, 1987–1992.

TABLE 1. Stage-based transition matrices for *Astragalus scaphoides* at two sites in 1987–1992. Four stages are recognized: dormant (D), small nonreproductive (S), large nonreproductive (L), and reproductive (R). The reproductive and recruitment (Rc) columns must be added together before solving for λ, the dominant eigenvalue (see Methods).

Sheep Corral Gulch

1987–88

	From				
To	D	S	L	R	Rc
D	.67	.18	.20	0	+ 0
S	.11	.55	.24	0	+ 0
L	.22	.06	.36	0	+ 0
R	0	0	.03	1.0	+ 0

$\lambda = 1.18$

1988–89

	From				
To	D	S	L	R	Rc
D	.23	.04	.02	0	+ 0
S	.17	.27	.05	0	+ 4.0
L	.43	.53	.45	0	+ 7.0
R	.17	.08	.43	1.00	+ .25

$\lambda = 2.51$

1989–90

	From				
To	D	S	L	R	Rc
D	.80	.17	.14	.06	+ 0
S	.10	.73	.37	.22	+ .91
L	.10	.02	.35	.56	+ .03
R	0	.02	.01	.16	+ 0

$\lambda = 0.97$

1990–91

	From				
To	D	S	L	R	Rc
D	.14	.06	0	0	+ 0
S	.21	.23	.06	0	+ 9.86
L	.50	.42	.26	.29	+ 2.42
R	.14	.12	.57	1.0	+ .14

$\lambda = 2.69$

1991–92

	From				
To	D	S	L	R	Rc
D	.70	.24	.21	.25	+ 0
S	.30	.27	.37	.33	+ .20
L	0	0	.14	.22	+ 0
R	0	0	0	0	+ 0

$\lambda = 0.83$

Haynes Creek

1987–88

	From				
To	D	S	L	R	Rc
D	.50	.03	.04	0	+ 0
S	.40	.45	.04	0	+ 5
L	0	.24	.37	0	+ .16
R	.10	.06	.52	.60	+ .20

$\lambda = 1.88$

1988–89

	From				
To	D	S	L	R	Rc
D	.57	.13	.04	0	+ 0
S	.14	.42	.24	.05	+ 1.10
L	.14	.16	.28	.14	+ .14
R	.14	.04	.32	.67	+ .05

$\lambda = 1.13$

1989–90

	From				
To	D	S	L	R	Rc
D	.64	.12	.05	0	+ 0
S	.27	.38	.14	.04	+ .23
L	0	.20	.48	.27	+ .04
R	.09	0	.33	.58	+ 0

$\lambda = 0.97$

1990–91

	From				
To	D	S	L	R	Rc
D	.21	.03	0	0	+ 0
S	.21	.34	.03	0	+ .95
L	.50	.31	.21	.18	+ .27
R	.07	.19	.66	.64	+ 0

$\lambda = 1.31$

1991–92

	From				
To	D	S	L	R	Rc
D	.75	.03	.06	.05	+ 0
S	0	.44	.30	.15	+ .30
L	.25	.08	.36	.53	+ .03
R	0	0	.11	.20	+ 0

$\lambda = 0.83$

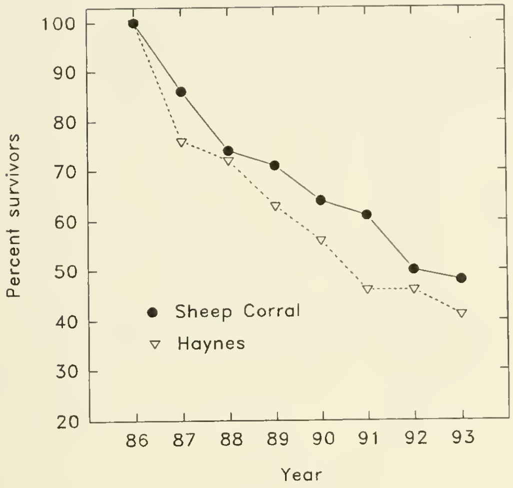

Fig. 2. Depletion curves for the 1986 sample populations of *Astragalus scaphoides* at the two study sites.

51% and 44% at Haynes Creek and Sheep Corral Gulch, respectively (Fig. 3).

Elasticity Analysis

Elasticity gives the proportional importance of demographic transitions to population growth. Elasticity matrices for five years of transitions for the two study sites are given in Table 2. Elasticities were summed into four life-history transition categories: (1) recruitment and survival and growth of (2) dormant, (3) nonreproductive, and (4) reproductive plants (Fig. 4). Growth and survival of nonreproductives was consistently important at both sites, with mean elasticities of 42% and 36% at Haynes Creek and Sheep Corral Gulch, respectively. Survival of dormant plants was important in two years at Sheep Corral Gulch and one year at Haynes Creek, with mean elasticities of 19% and 29%. Survival of reproductives had mean elasticities of 23% and 20% for the two sites, and mean elasticities for recruitment were 16% and 17%.

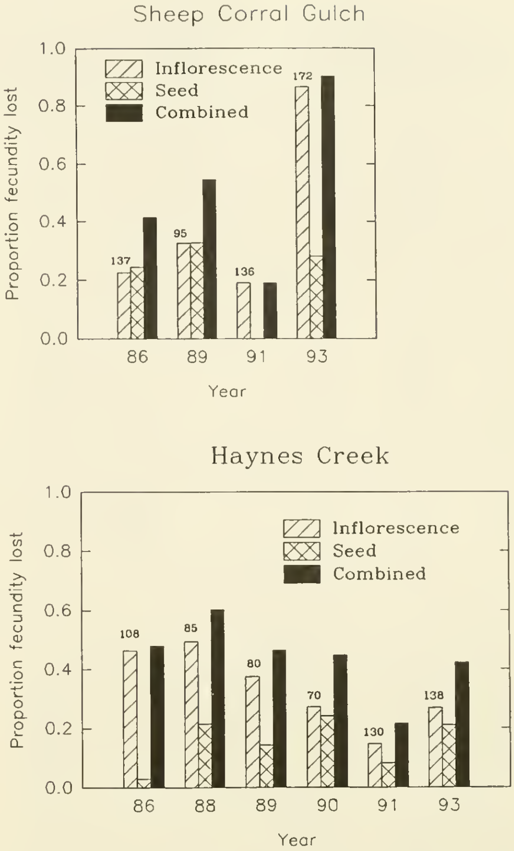

Fig. 3. Proportion of *Astragalus scaphoides* reproductive output lost to inflorescence predation, predispersal seed predation, and the combination of the two in those years when significant flowering occurred at two study sites. Numbers of inflorescences in samples are given above bars.

DISCUSSION

Loss of *Astragalus scaphoides* fecundity due to inflorescence and predispersal seed predation was high at both sites, ranging from ca 20% to >90%. Further losses in reproductive output due to ants or rodents may have occurred following dispersal. Recruitment was the least important stage transition in the life history of *A. scaphoides* during my study, accounting for an average of less than 17% of population growth at both sites. High levels of inflorescence and seed herbivory are undoubtedly one of the main reasons for the low contribution of recruitment to λ in this species. Nonetheless, both sample populations became larger during the study. Furthermore, population growth rate was ≳1.0 in four of five years at both sites and never <0.8. Growth and survival of dormant and nonreproductive plants contributed >60% to population growth at both sites. These results suggest that populations of *A. scaphoides* can persist and even grow larger in spite of heavy losses in reproductive output and low recruitment.

Large reductions in fecundity due to herbivores have been documented for *Astragalus* species (Green and Palmbald 1975) as well as

TABLE 2. Elasticities for *Astragalus scaphoides* stage transition matrices at two sites for 1987–1992. The left three columns (D, S, L) represent nonreproductive growth and survival. The reproductive (R) column represents growth and survival of reproductives. The recruitment column (Rc) represents recruitment from seed.

Sheep Corral Gulch

1987–88

	D	S	L	R	Rc
D	.048	.022	.015	0	0
S	.004	.032	.009	0	.024
L	.032	.015	.055	0	.077
R	0	0	.101	.568	0

1988–89

	D	S	L	R	Rc
D	.001	.003	.001	0	0
S	.001	.017	.002	0	.139
L	.002	.081	.049	0	.143
R	.003	.057	.222	.224	.056

1989–90

	D	S	L	R	Rc
D	.413	.074	.015	.001	0
S	.048	.292	.037	.002	.011
L	.042	.007	.030	.005	.001
R	0	.017	.002	.004	0

1990–91

	D	S	L	R	Rc
D	.001	.005	0	0	0
S	.001	.018	.002	0	.185
L	.002	.082	.023	.014	.118
R	.003	.099	.215	.204	.029

1991–92

	D	S	L	R	Rc
D	.686	.126	0	0	0
S	.126	.061	0	0	0
L	0	0	0	0	0
R	0	0	0	0	0

Haynes Creek

1987–88

	D	S	L	R	Rc
D	.002	.003	.002	0	0
S	.001	.045	.002	0	.141
L	0	.082	.058	0	.153
R	.003	.059	.231	.164	.055

1988–89

	D	S	L	R	Rc
D	.055	.048	.006	0	0
S	.007	.086	.020	.005	.113
L	.015	.064	.044	.028	.028
R	.031	.034	.109	.287	.021

1989–90

	D	S	L	R	Rc
D	.081	.028	.013	0	0
S	.023	.061	.024	.007	.039
L	0	.065	.170	.093	.014
R	.018	0	.134	.230	0

1990–91

	D	S	L	R	Rc
D	.001	.005	0	0	0
S	.001	.058	.004	0	.160
L	.004	.080	.038	.046	.068
R	.001	.079	.193	.264	0

1991–92

	D	S	L	R	Rc
D	.617	.020	.041	.006	0
S	0	.042	.030	.003	.005
L	.068	.018	.082	.021	.001
R	0	0	.036	.011	0

many other plants (Janzen 1971, Hendrix 1988, Louda 1989). Louda (1982, 1983) has shown that seed predation can lead to lowered recruitment; however, reductions in seed output will not necessarily lead to reduced recruitment if germination safe sites are limiting (Harper 1977). Analysis of the matrix projection models suggests that recruitment is not limiting population growth of *A. scaphoides*.

Recruitment from seed is likely to be important to population growth for short-lived species and is essential for semelparous ones. Furthermore, successful reproductive episodes are rare for some perennial species in rigorous environments (Jordan and Nobel 1979). Significant reductions in a single reproductive bout could greatly increase chances of population extirpation for these sorts of species. On the other hand, many populations of long-lived plants will have more stable populations whose persistence is more dependent on the growth and survival of established plants (Silvertown et al. 1993). Survivorship curves indicate that *Astragalus scaphoides* is a long-lived species, and elasticity analysis suggests that recruitment is indeed less important to population persistence than growth and survival of nonreproductive plants.

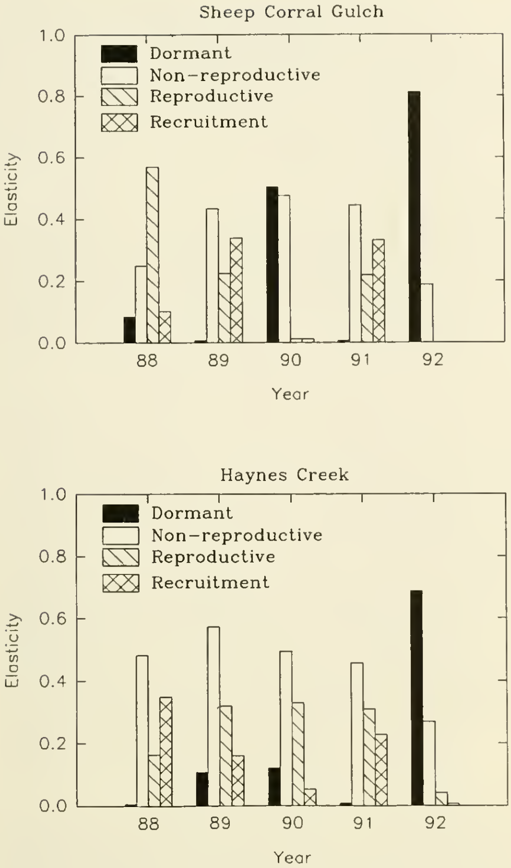

Fig. 4. Elasticities summed into four life-history transition categories (recruitment and survival and growth of dormant, nonreproductive, and reproductive plants) for *Astragalus scaphoides* at two study sites, 1987–1992.

Inflorescence predation of *Astragalus scaphoides* was greatest in years when livestock were present. In 1993 inflorescence predation was greater than 85%, and *A. scaphoides* was grazed in preference to the highly palatable grass, *Agropyron spicatum* (P. Lesica personal observation). These observations suggest that livestock could nearly eliminate reproductive output under high stocking rates and repeated heavy spring grazing if carried on over a long enough period of time. However, results of my study suggest that *A. scaphoides* populations can persist if predation is moderate, at least in some years. Rotation grazing systems in which spring grazing occurs only one in three years appear to be compatible with the long-term persistence of *A. scaphoides* populations.

These results have implications for other long-lived perennials exposed to livestock predation. Upper portions of plants are most accessible to livestock, and newer growth is generally selected by livestock (Arnold and Dudzinski 1978, Valentine 1990). Furthermore, sugars, such as found in flower nectar, also increase palatability (Arnold and Dudzinski 1978, Valentine 1990). Thus, livestock often remove only the upper portions of broad-leaved plants. Predation that mainly affects fecundity is likely to endanger populations only when grazing removes most inflorescences consistently for many years because population growth is not likely to be limited by recruitment. On the other hand, grazing that lowers growth and survival (e.g., high-density stocking during periods of growth) will have a much more detrimental effect on population viability.

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LAHONTAN SAGEBRUSH (*ARTEMISIA ARBUSCULA* SSP. *LONGICAULIS*): A NEW TAXON

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ABSTRACT.—A new subspecies of *Artemisia arbuscula* is described, *A. arbuscula* ssp. *longicaulis* Winward & McArthur, ssp. nov. This taxon is a landscape dominant in portions of northwestern Nevada and adjacent California and Oregon at elevations from 1050 to 2000 m on shallow or argillic (clayey) soils. It differs from *A. arbuscula* ssp. *arbuscula* in its long floral stalks and large leaves. Morphological, chemical, ecological, and cytological data suggest that it is of hybrid origin. It is hexaploid (6x). We hypothesize that 2x *A. arbuscula* ssp. *arbuscula* and 4x *A. tridentata* ssp. *wyomingensis* are its parents.

Key words: Nevada, taxonomy, chemotaxonomy, allopolyploid, hybrid, Tridentatae.

In preliminary reports we (Winward et al. 1986, 1991) provided a brief description of a new taxon of *Artemisia* found in northwestern Nevada and adjacent California and Oregon. We suggested referencing it by the common name Lahontan sagebrush pending a formal description. This paper provides that formal description and details concerning its taxonomy, distribution, general ecology, and origin.

TAXONOMY

The new taxon is a member of subgenus *Tridentatae* of *Artemisia*, the true sagebrushes (Beetle 1960, McArthur et al. 1981, Shultz 1986). We suggested (Winward et al. 1986) that this taxon may have originated as a hybrid with parental lines consisting of low and big sagebrush (*A. arbuscula* and *A. tridentata*). Because of its general morphology and ecology, we suggested that it be considered a subspecies of *A. arbuscula*. Further studies indicate that this new taxon is in fact best treated as a subspecies of *A. arbuscula*.

The type specimen of *A. arbuscula* came from a collection along the arid plains of the Lewis (now known as the Snake) River (Nuttall 1841). Subsequent workers have submerged the species as a subspecies of big sagebrush, *A. tridentata* ssp. *arbuscula* (Hall and Clements 1923), or, in contrast, recognized a number of races and subspecies within the species (Ward 1953, Beetle 1960). Ward proposed that black sagebrush (*A. nova*) was best treated as a subspecies of *A. arbuscula*, but Beetle (1960) restored it to Nelson's (1900) original species status. Beetle (1960) recognized two subspecies of *A. arbuscula*, *arbuscula* and *thermopola*. His treatment has been generally accepted (Winward and Tisdale 1977, McArthur et al. 1981, Shultz 1986), although Winward (1980) has observed an unusual variant of *A. arbuscula* in eastern Oregon that reaches a height of 1 m. He suggested that further taxonomic treatment of *A. arbuscula* would be appropriate.

During the past few decades fieldworkers in western Nevada have observed a sagebrush that does not fit the existing *Artemisia* taxonomic keys. Brunner (1972) termed this sagebrush "wide-lobe" with the comment, "Dr. Beetle feels this may be an ecotype of *A. tridentata* ssp. *wyomingensis*. I concur." Others have referred to it as "wonder sagebrush," "junk sagebrush," or "N" sagebrush (Winward et al. 1986). Accessions of two populations (Trough Springs, Humboldt County, NV, cultures U1 and U58 and Leonard Creek, Humboldt County, NV, culture U55) of this taxon were established in common gardens of the Forest Service's Shrubland Biology and Restoration Research Work Unit at several locations around central Utah; there they were treated as an ecotype of *A. tridentata* ssp. *wyomingensis* following Beetle and Brunner (Brunner 1972;

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e.g., McArthur and Plummer 1978, Welch and McArthur 1979, 1981, 1986, McArthur et al. 1981, 1985, McArthur and Welch 1982, Welch et al. 1986, 1987). The new taxon is a landscape dominant over much of its range (Winward et al. 1986), and both domestic and wild animals feed extensively on it (Brunner 1972, Welch and McArthur 1986, Winward et al. 1986, Welch et al. 1987).

Description

Artemisia arbuscula ssp. *longicaulis* Winward & McArthur ssp. nov. Similis *A. arbuscula* ssp. *arbuscula* sed ramis floralibus multo longioribus et foliis magnioribus differt (Similar to *A. arbuscula* ssp. *arbuscula* except flower stalks are much longer and leaves are larger).

The longer flower stalks and larger leaves also differentiate ssp. *longicaulis* from ssp. *thermopola*, which differs from ssp. *arbuscula* and *longicaulis* by having deeply trifid leaves (Beetle 1959).

We chose the common name Lahontan sagebrush because the old shorelines of Pleistocene Lake Lahontan are one of the centers of its current distribution and may have provided the ecological setting for the taxon's origin and development (Winward et al. 1986, 1991).

Type: Toulon, Pershing County, Nevada, USA, 1053 m, S. C. Sanderson and E. D. McArthur 1593, 21 August 1986. Holotype: BRY. Isotypes: OGDF, RENO, SSLP, and UTC. Other specimens examined:

- Nevada, Douglas Co., Topaz Lake, Sanderson & McArthur 1594, (SSLP, four sheets);
- Nevada, Humboldt Co., Golconda, Plummer *s.n.*, 1985, (SSLP);
- Nevada, Humboldt Co., Leonard Creek, Plummer & McArthur, *s.n.*, 3 October 1975, culture U55, (SSLP);
- Nevada, Humboldt Co., Trough Springs, Jackson Mountains, Plummer, Brunner, & McArthur, *s.n.*, 3 October 1975, culture U1, (SSLP);
- Nevada, Humboldt Co., Trough Springs, Jackson Mountains, McArthur 1532, culture U1, (SSLP);
- Nevada, Humboldt Co., Trout Creek Basin, Jackson Mountains, McArthur 1501, (SSLP, two sheets);
- Nevada, Lyon Co., Dayton, Sanderson & McArthur 1595, (SSLP, two sheets);
- Nevada, Pershing Co., 6.4 km west of Toulon, McArthur & McArthur 1683, (SSLP, two sheets);
- Nevada, Washoe Co., Mustang, McArthur & McArthur 1684, (SSLP);
- Oregon, Lake Co., 32 km east of Adell, Sanderson & McArthur 1590, (SSLP);
- Oregon, Malheur Co., near McDermitt, Nevada, Winward, *s.n.* 31 October 1986, (OGDF, two sheets, SSLP).

DISTRIBUTION AND ECOLOGY

Artemisia arbuscula ssp. *longicaulis* occurs on several hundred thousand hectares in northwestern Nevada and in adjacent areas of California and Oregon at elevations from about 1050 to 2000 m (Fig. 1). It often occurs in pure stands. It may also share dominance with other sagebrush taxa such as big sagebrush (*A. tridentata* ssp. *tridentata* and *wyomingensis*), low sagebrush (*A. arbuscula* ssp. *arbuscula*), and black sagebrush (*A. nova*). At lower elevations it is interspersed with salt desert shrub species such as shadscale (*Atriplex confertifolia*), Bailey greasewood (*Sarcobatus baileyi*), Mormon tea (*Ephedra* spp.), budsage (*Artemisia spinescens*), Shockley's desert thorn (*Lycium shockleyi*), and horsebrush (*Tetradymia* spp.). Except for *Artemisia*, our taxonomy follows Welsh et al. (1993) and Mozingo (1987). The most common grass understory species at upper-elevation Lahontan sagebrush sites is bluebunch wheatgrass (*Elymus spicatus*). At lower elevations Thurber and desert needlegrasses (*Stipa thurberiana* and *S. speciosa*), and Indian ricegrass (*Stipa hymenoides*), bottlebrush squirreltail (*Elymus elymoides*), and Sandberg bluegrass (*Poa secunda*) are more common. Areas supporting *A. arbuscula* ssp. *longicaulis* receive between 175 and 350 mm of precipitation annually with most as winter precipitation. The frost-free season ranges from 90 to 110 days. Lahontan sagebrush grows most commonly on Aridisols, but at upper elevations it also occurs on Mollisols. Soil Conservation Service, U.S. Department of Agriculture, personnel have located *A. arbuscula* ssp. *longicaulis* on at least 17 soil series. Generally, these soils have low available water-holding capacities and a shallow depth to an argillic horizon and/or bedrock. These soils are similar to those of low sagebrush (*A. arbuscula* ssp. *arbuscula*) communities

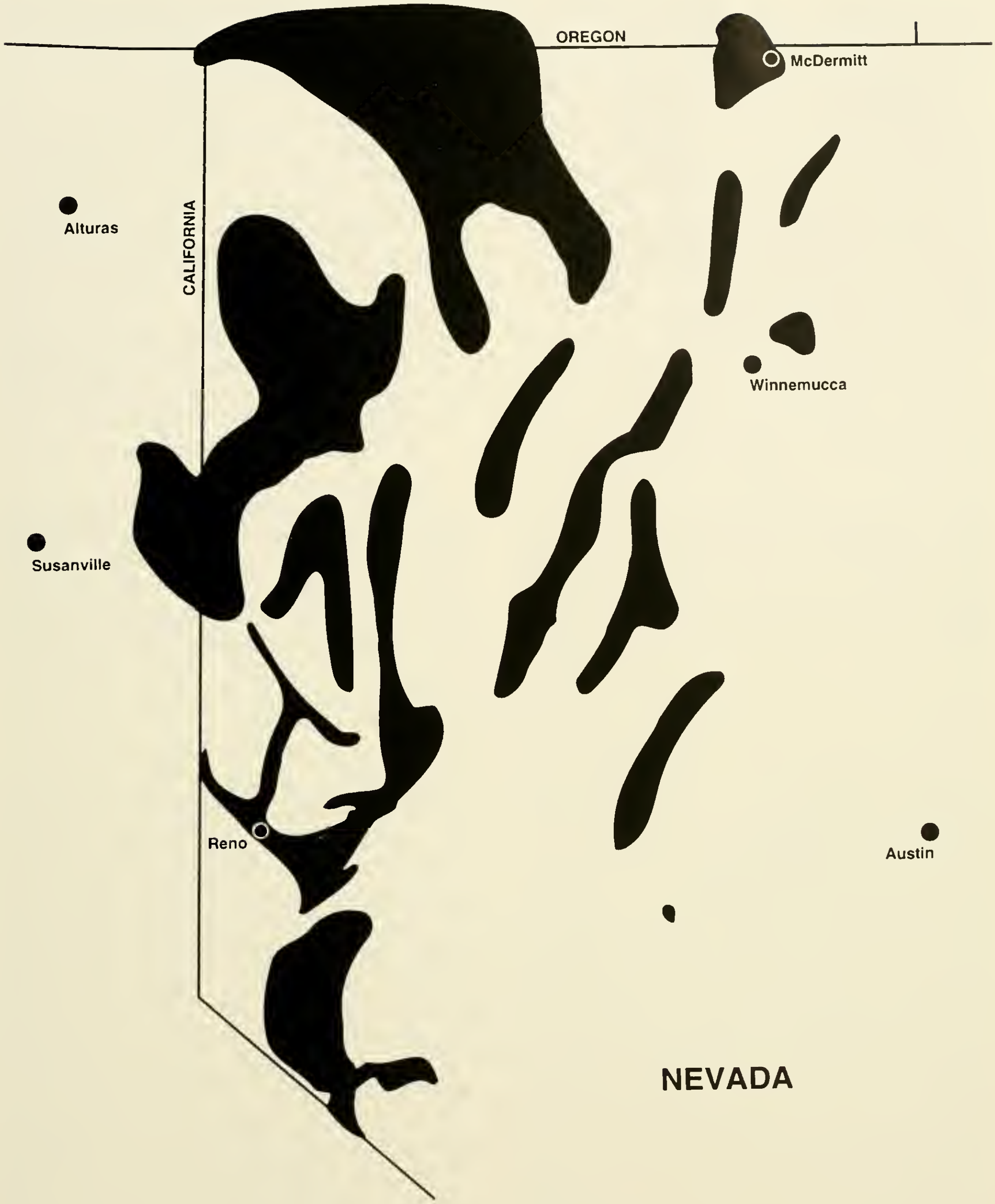
OREGON
McDermitt
Alturas
CALIFORNIA
Winnemucca
Susanville
Reno
Austin
NEVADA

Fig 1. Extent of the known distribution of *Artemisia arbuscula* ssp. *longicaulis*.

(Fosberg and Hironaka 1964, Zamora and Tueller 1973, G. K. Brackley and C. A. Plummer personal communication).

General distributions of the three subspecies of *A. arbuscula* are as follows: ssp. *arbuscula*, western Wyoming and eastern Utah to eastern Washington and northeastern California; ssp. *thermopola*, western Wyoming and adjacent Idaho and northern Utah to northern Nevada and eastern Oregon; ssp. *longicaulis*, western Nevada, extending into adjacent California and Oregon.

SUPPORTING DATA AND DISCUSSION

Morphological, chemical, and cytological data are consistent with the hypothesis that *A. arbuscula* ssp. *longicaulis* is of hybrid origin, with *A. arbuscula* ssp. *arbuscula* as one parent and *A. tridentata* ssp. *wyomingensis* as the other parent. Hybridization and introgression are thought to have been important in the evolutionary development and differentiation of *Tridentatae* taxa (Ward 1953, Beetle 1960, McArthur et al. 1981, 1988). The following taxa are thought to have originated as hybrids:

- *A. argillosa* (*A. cana* ssp. *viscidula* × *A. longiloba*—Beetle 1959),
- *A. tridentata* ssp. *spiciformis* (*A. tridentata* ssp. *vaseyana* × *A. cana* ssp. *viscidula*—Beetle 1959, Goodrich et al. 1985, McArthur and Goodrich 1986),
- *A. tridentata* ssp. *xericensis* (*A. tridentata* ssp. *tridentata* × *A. tridentata* ssp. *vaseyana*—Winward 1970, Rosentreter and Kelsey 1991),
- *A. tridentata* ssp. *wyomingensis* (*A. tridentata* ssp. *tridentata* × *A. tridentata* ssp. *vaseyana* with perhaps some involvement with *A. nova* as well—Beetle and Young 1965, Winward 1975, McArthur 1983).

Figure 2 shows a polygonal representation of morphological features of the new subspecies and its putative parents, including permanent leaf width, length, and length/width ratio and flower and vegetative stalk lengths. Values are shown in Table 1. Morphological differences

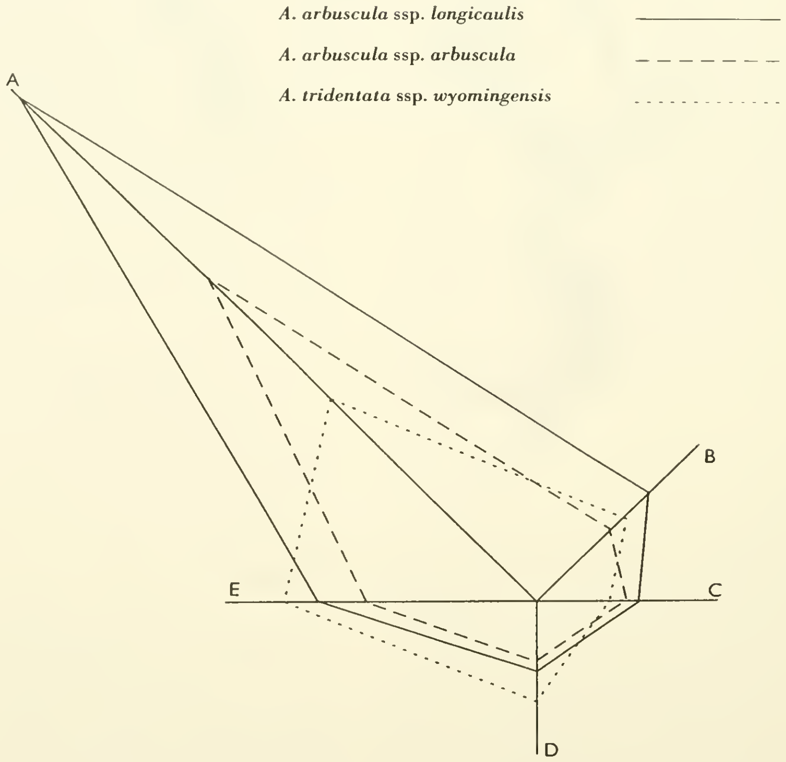

Fig. 2. Polygonal graph comparing morphological features of *Artemisia arbuscula* ssp. *longicaulis* and its putative parents, *A. arbuscula* ssp. *arbuscula* and *A. tridentata* ssp. *wyomingensis*. Data from Table 1: A = flower stalk length; B = vegetative stalk length; C = leaf width; D = leaf l/w ratio; E = leaf length.

TABLE 1. Morphological measurements (means ± SD) of *A. arbuscula* ssp. *arbuscula* (ARAR^a), *A. arbuscula* ssp. *longicaulis* (ARAR^l), and *A. tridentata* ssp. *wyomingensis* (ARTR^w)[a].

	ARAR^a	ARAR^l	ARTR^w
Flower stalk length (cm)	16.4 ± 1.7	24.5 ± 3.4	10.4 ± 4.2
Vegetative stalk length (cm)	3.9 ± 0.8	5.7 ± 1.2	4.7 ± 2.4
Leaf length (mm)	5.9 ± 1.1	7.3 ± 1.0	8.3 ± 2.4
Leaf width (mm)	3.0 ± 0.4	3.4 ± 0.4	2.7 ± 0.8
Leaf l/w ratio	2.0	2.2	3.1

[a] Data for ARAR^a are from the following collections: California, Lassen Co., Shaffer Mountain, Sanderson & McArthur 1591 (SSLP); Nevada, Eureka Co., Tuscarora Mountains, 40 km north of Carlin, Frischknecht 210, (SSLP); Nevada, Humboldt Co., 13 km northwest of Paradise Valley Town, Holmgren 128, (SSLP); Nevada, Lander Co., Bade Creek, Toiyabe National Forest, Goodrich 8868, (OGDF); Nevada, Lander Co., Toiyabe Range, Toiyabe National Forest, Goodrich 9966, (OGDF); Nevada, Nye Co., Toiyabe Range, Toiyabe National Forest, Goodrich 12201, (OGDF); Nevada, Pershing Co., 40 km northeast of Winnemucca, Winward *s.n.*, 25 October 1984, (OGDF); Nevada, Washoe Co., Buffalo Hills, 40 km northwest of Gerlach, Sanderson & McArthur 1592, (SSLP).

Data for ARAR^l are from collections: Nevada, Humboldt Co., Golconda, Plummer *s.n.*, 1985, (SSLP); Nevada, Humboldt Co., Trough Springs, McArthur 1532, (SSLP); Nevada, Humboldt Co., Trout Creek Basin, McArthur 1501, (SSLP); Nevada, Pershing Co., Toulon, Sanderson & McArthur 1593, (SSLP); Nevada, Pershing Co., 6.4 km. west of Toulon, McArthur & McArthur 1683, (SSLP); Nevada, Washoe Co., Mustang, McArthur & McArthur 1684, (SSLP); Oregon, Lake Co., 32 km east of Adell, Sanderson & McArthur 1590, (SSLP); Oregon, Malheur Co., near McDermitt, Nevada, Winward *s.n.*, 31 October 1986, (OGDF).

Means for each taxa are based on $N = 8$. Differences are significant by one-way analysis of variance (Woolf 1969) for flower stalk length ($P < .01$), vegetative stalk length ($P < .05$), and leaf length ($P < .01$) between ARAR^a and ARAR^l. Data for ARTR^w are from Winward (1970). Means from ARTR^w were not statistically compared with the other taxa.

may be summarized as follows: (1) Flower stalk length averages 50% longer for *A. arbuscula* ssp. *longicaulis* than for *A. arbuscula* ssp. *arbuscula* and over twice as long as *A. tridentata* ssp. *wyomingensis.* (2) *A. tridentata* ssp. *wyomingensis* has longer, narrower leaves than the other taxa. (3) *A. arbuscula* ssp. *longicaulis* has larger leaves and a longer vegetative stalk than *A. arbuscula* ssp. *arbuscula.*

Wilt et al. (1992) compared 34 phenolic compounds from six taxa of *Tridentatae* including *A. tridentata* ssp. *wyomingensis, A. arbuscula* ssp. *longicaulis* (undescribed at the time and called by them "Lahontan" sagebrush), and *A. arbuscula* ssp. *arbuscula.* Their work demonstrated that typical high-pressure liquid chromatography patterns for *A. arbuscula* ssp. *longicaulis* and *A. tridentata* ssp. *wyomingensis* are remarkably similar (their Fig. 2). Representative chromatograms of those two taxa are the most similar of the six taxa studied (*A. arbuscula* ssp. *arbuscula, A. nova, A. tridentata* ssp. *tridentata, A. t.* ssp. *vaseyana, A. t.* ssp. *wyomingensis,* and "Lahontan" sagebrush; Wilt et al. 1992). We analyzed the Wilt et al. (1992) frequency of detection of individual phenolics by assigning percent similarity values for each shared phenolic (Table 2). Those values are not dramatically different for *A. arbuscula* ssp. *longicaulis* in respect to the other five taxa, but *A. arbuscula* ssp. *arbuscula* and *A. tridentata* ssp. *wyomingensis* are the two most similar (at 54%) to *A. arbuscula* ssp. *longicaulis.* For total phenolics the Wilt et al. (1992) data are very close for *A. arbuscula* ssp. *longicaulis* and *A. t.* ssp. *wyomingensis,* closer than for any other two taxa examined.

A. arbuscula ssp. *longicaulis* is hexaploid, $6x = 2n = 54$. McArthur et al. (1981) reported this taxon as *A. tridentata* ssp. *wyomingensis* "wide-lobe" and gave chromosome counts as $2n = 36, 54$ for two transplanted population samples growing in a common garden. We now suspect both bona fide *A. tridentata* ssp. *wyomingensis* and *A. arbuscula* ssp. *longicaulis* were growing in the accessional rows.

A. tridentata ssp. *wyomingensis* is uniformly tetraploid, $2n = 36$ for the ca 70 populations that have been examined, and *A. arbuscula* ssp. *longicaulis* is uniformly hexaploid, $n = 27$ for seven populations including Trout Creek (McArthur 1501), Adell (Sanderson and McArthur 1590), Toulon (Sanderson and McArthur 1593), Topaz Lake (Sanderson and McArthur 1594), Dayton (Sanderson and McArthur 1595), and Mustang (McArthur and McArthur 1684) populations cited earlier in this report (McArthur et al. 1981, McArthur and Sanderson in review).

Morphological, chemical, and cytological evidence reveals affinities of *A. arbuscula* ssp. *longicaulis* for both *A. a.* ssp. *arbuscula* and *A. tridentata* ssp. *wyomingensis.* In a series of common garden experiments (Hanks et al. 1973, McArthur and Plummer 1978, Welch and McArthur 1979, 1981, 1986, Nelson and Krebill 1981, McArthur et al. 1981, McArthur and Welch 1982, Welch et al. 1987), Lahontan sagebrush accessions (U1 and U58—Trough Springs, NV, and U55—Leonard Creek, NV) were treated as Wyoming big sagebrush. They fit with that group in those experiments.

Sagebrush taxa hybridize naturally (McArthur et al. 1988). We propose that *A. arbuscula* ssp.

TABLE 2. Percent frequency of shared phenolics for *A. nova* (ARNO), *A. tridentata* ssp. *tridentata* (ARTR^{t}), *A. tridentata* ssp. *vaseyana* (ARTR^{v}), *A. tridentata* ssp. *wyomingensis* (ARTR^{w}), *A. arbuscula* ssp. *arbuscula* (ARAR^{a}), and *A. arbuscula* ssp. *longicaulis* (ARAR^{l}); data from Wilt et al. (1992).

	ARNO	ARTR^{t}	ARTR^{v}	ARTR^{w}	ARAR^{a}	ARAR^{l}
ARNO		52	49	57	59	52
ARTR^{t}			52	76	48	52
ARTR^{v}				48	58	53
ARTR^{w}					52	54
ARAR^{a}						54

longicaulis is an allopolyploid derivative from diploid, $n = 9$, *A. arbuscula* ssp. *arbuscula*, and tetraploid, $n = 18$, *A. tridentata* ssp. *wyomingensis*. *A. arbuscula* ssp. *arbuscula* occurs in both diploid and tetraploid populations in the northwestern Nevada area. Tetraploid *A. tridentata* ssp. *wyomingensis* also occurs there (McArthur and Sanderson in review). Population dynamics of sagebrush populations migrating in response to climatic change during the various phases of ancient Lake Lahontan and other pluvial lakes of the Lahontan basin (Morrison 1965) could have provided the opportunity for the origin and establishment of *A. arbuscula* ssp. *longicaulis*. Morphological, cytological, and chemical data are consistent with the hybrid origin hypothesis.

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DOUGLAS-FIR TUSSOCK MOTH (*ORGYIA PSEUDOTSUGATA* MCDUNNOUGH) ON SUBALPINE FIR IN NORTHERN UTAH

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ABSTRACT.—Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) defoliation was detected by aerial survey on three areas of the Wasatch-Cache National Forest in 1990 and 1991. These are the first documented tussock moth outbreaks in Utah. Ground surveys revealed that subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) was heavily defoliated during the outbreak. Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), though a minor component in the affected areas, had noticeably less defoliation and mortality. Adjacent stands of Douglas-fir had little or no visible tussock moth activity. Defoliation on subalpine fir was typically found evenly distributed throughout the crown rather than concentrated at the top. Ninety-four percent of subalpine fir with defoliation ratings of 90% or more were killed. Top-kill occurred on nearly one-half of subalpine firs defoliated 25–89%. Heavily defoliated trees tended to occur in pockets bounded by areas of light defoliation. After three consecutive years of defoliation, tussock moth populations collapsed. No life stages were detected in 1993 from visual inspections of foliage or in pheromone traps.

Key words: tussock moth, subalpine fir, defoliators, Douglas-fir, Utah forests, forest insects.

The Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) is a significant defoliator of Douglas-fir and true firs throughout its host range in western North America. Tussock moth outbreaks on the Wasatch-Cache National Forest, UT, from 1990 to 1992 were unique because subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) experienced greater defoliation and mortality than Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco). These tussock moth infestations are the first documented outbreaks in Utah (Ollieu 1978, Tunnock et al. 1985).

Previous tussock moth outbreaks indicate three primary hosts depending on location. In British Columbia and northern Washington, Douglas-fir is preferred; in southern Washington, Oregon, and Idaho, Douglas-fir, white fir (*Abies concolor* [Gord. and Glend.]), and grand fir (*A. grandis* [Dougl.] Lindl.) are preferred; in California, Nevada, Arizona, and New Mexico, white fir is preferred (Wickman et al. 1981). In these areas subalpine fir and other members of the pine family are typically defoliated after the preferred host is consumed. The Wasatch-Cache National Forest outbreaks experienced light defoliation of Douglas-fir within stands of completely defoliated subalpine fir.

Interestingly, the first record of tussock moth defoliation in the United States was on subalpine fir at Jarbidge, NV, in 1927 (Balch 1930). Affected areas were of subalpine fir occurring either purely or in mixture with limber pine (*Pinus flexilis* James). These two conifers and quaking aspen (*Populus tremuloides* Michx.) formed virtually the entire forest at Jarbidge (Balch 1932) in contrast to the Utah sites that contain or are surrounded by substantial Douglas-fir. Balch's records are the only literature indicating subalpine fir to be a principal host, while more recent authors consider the species to be secondary (Wickman et al. 1981, Berryman 1988).

The objective of this study was to document the effects of these outbreaks on subalpine fir. Information will be used to predict future impacts of tussock moth defoliation on subalpine fir resource. This report summarizes stand conditions following infestation and attempts to characterize the effects of defoliation on individual trees.

METHODS

Aerial detection surveys delineated tussock moth activity near the Baxter Sawmill site, Ogden Ranger District, Wasatch-Cache National Forest, UT, in 1990. Additional infestations were detected at Blind Hollow and Amazon Hollow, Logan Ranger District, Wasatch-Cache National Forest, UT, in 1991. Subsequent ground surveys confirmed tussock moth populations at these locations.

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A total of 35 pairs of 20 basal-area-factor variable plots and 1/300 ac seedling/sapling fixed plots were established in July 1992 at the three areas. Plots were installed along a transect at 100-m intervals starting from a reference point in areas with visible defoliation. No other attempt was made to randomize plot locations or to cover the entire affected area. Tree data collected include species, diameter at breast height (DBH), height, age, 5- and 10-year radial growth, insect/disease damage, and an ocular estimate of percent defoliation. Additionally, the distal 18 inches of three randomly selected lower crown branches on all host species were examined for pupae or egg masses.

Plots were remeasured in July 1993 to evaluate changes in insect-related tree injury and mortality, percent defoliation, and presence of tussock moth life stages. One pair of plots at Baxter Sawmill was cut and lost during salvage operations. To maximize data-collection consistency, the same individual conducted defoliation estimates on 32 of 35 plots for plot establishment and remeasurement.

INDIDS, the insect and disease damage survey program (Bousfield et al. 1985), was used to calculate per-acre average stand characteristics. Individual tree defoliation ratings were classified into the five categories of Weatherby et al. (1992): (1) undamaged, (2) lightly defoliated (1–24% of total needle complement defoliated), (3) moderately defoliated (25–74%), (4) heavily defoliated (75–89%), and (5) very heavily defoliated (90+%). Defoliation ratings from 1992 and 1993 were used to determine defoliation effects on tree condition.

RESULTS

Blind Hollow

Prior to the outbreak, composition of all live trees greater than 5 inches DBH was 69% subalpine fir, 28% aspen, and 3% Douglas-fir. Total pre-outbreak live basal area was 178.9 sq ft/ac. By 1993 live basal area was reduced to 166.8 sq ft/ac. Site elevations range from 7800 to 8100 ft. Aspect ranges from southwest to south to east on slopes varying from 10 to 50%.

Subalpine fir seedlings and saplings (0–4.9 inches DBH) were significantly affected by tussock moth. Sixty stems per acre in this size class representing 25% of the stocking were killed (Table 1). Pole-sized subalpine fir (5–8.9 inches DBH) were more frequently defoliated than larger diameter classes. Fifty-eight percent of stems 5–8.9 inches DBH, 34% of stems 9–11.9 inches DBH, and 39% of stems ≥12 inches DBH were defoliated. Stems exhibiting top-kill increased proportionately with percent defoliation. Four percent of subalpine fir stems over 5 inches DBH were killed by tussock moth.

In the ≥12-inches diameter class, none of 7.3 Douglas-fir per acre were visibly defoliated (Table 1). Among subalpine fir in this class, 3% of 65.1 per acre were defoliator killed. Twenty-eight percent survived defoliation, while 69% were not visibly defoliated.

Western balsam bark beetle (*Dryocoetes confusus* Swaine) killed 4.9 subalpine fir stems per acre. These trees were attacked in 1991, coinciding with the peak of the tussock moth outbreak.

TABLE 1. Trees per acre condition summary of subalpine fir and Douglas-fir following a Douglas-fir tussock moth outbreak, Blind Hollow, Wasatch-Cache National Forest, July 1993. Summary calculated from 10 variable/fixed plot pairs. SAF = subalpine fir, DF = Douglas-fir.

	Defoliation class											
Diameter	Undamaged		Light		Moderate		Heavy		Very heavy		Mortality	
class	SAF	DF	SAF	DF	SAF	DF	SAF	DF	SAF	DF	SAF	DF
0–4.9″	30.0	0.0	120.0	0.0	30.0	0.0	0.0	0.0	0.0	0.0	60.0	0.0
5–8.9″	39.0	0.0	16.0	0.0	18.5	0.0	6.0	0.0	6.2	0.0	6.0	0.0
9–11.9″	25.9	2.9	7.0	0.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12″ +	40.0	7.3	13.4	0.0	4.8	0.0	0.0	0.0	0.0	0.0	2.1	0.0

The 1992 survey found an average of 3.1 pupae and 0.5 egg masses per three-branch samples. The 1993 survey found no current life stages on any sample tree, and no life stages were visible in the area.

Baxter Sawmill

Prior to the outbreak, composition for all live trees greater than 5 inches DBH was 65% subalpine fir, 25% aspen, and 10% Douglas-fir. Total live basal area was 176.1 sq ft/ac at the onset of the outbreak. Live basal area in 1993 was 112.8 sq ft/ac. Site elevations range from 7400 to 7900 ft. Aspect is south, southwest, west, and northwest on slopes varying from 10 to 30%.

Subalpine fir seedlings and saplings had considerable defoliator damage. More than 250 seedlings and saplings per acre, or 55% of stocking in this size class, died (Table 2). Most surviving seedlings and saplings were only lightly defoliated. Forty-nine percent of subalpine fir stems 5.0–11.9 inches DBH were killed by tussock moth. Trees with top-kill increased proportionately with percent defoliation. Only 3% of subalpine fir stems in the lightly defoliated category experienced top-kill, compared to 92% of surviving trees in the heavily and very heavily defoliated classes.

In the ≥12-inches diameter class, Douglas-fir had 10% of 22.6 trees per acre defoliator killed. Fifty-seven percent were not defoliated, with another 33% defoliated but surviving (Table 2). Among 38.5 subalpine fir per acre in this size class, 7% were defoliator killed and 77% were defoliated but survived.

Western balsam bark beetle has also been active at Baxter Sawmill, killing 38.2 subalpine fir per acre, mostly in 1990 or 1991. Annosus root disease (*Heterobasidion annosum* [Fr.] Bref.) was found on 4.6 subalpine fir per acre.

The 1992 survey found an average of 4.8 pupae and 1.2 egg masses per three branches sampled. No current life stages were found in 1993 on the plots or in the area. Additionally, no tussock moths were caught in pheromone traps placed in the Baxter Sawmill area in 1993.

Amazon Hollow

Prior to the outbreak, composition of all live trees greater than 5 inches DBH was 73% subalpine fir, 24% aspen, 2% Douglas-fir, and 1% lodgepole pine. Total live basal area was 125.5 sq ft/ac at the onset of the outbreak. Live basal area in 1993 was 72.2 sq ft/ac. Site elevations range from 7500 to 7800 ft. Aspect is east on slopes varying from 10 to 25%.

One-hundred subalpine fir seedlings and saplings per acre, or 10% of stocking in that class, were killed (Table 3). Mortality in the three size classes greater than 5 inches DBH ranged from 50 to 62%. Top-kill was common for all defoliation intensities. Of the surviving defoliated subalpine fir (>5 inches DBH), 60% had top-kill, including 63% of stems classified as lightly defoliated.

In the ≥12-inches size class, 28% of 4.3 Douglas-fir per acre were defoliator killed with another 16% defoliated but surviving (Table 3). Among 29.7 subalpine fir per acre in that class, 50% were defoliator killed and another 31% were defoliated but survived.

Western balsam bark beetle killed 2.6 subalpine fir per acre. Annosus root disease was found on 4.2 trees per acre.

The 1992 survey found 2.0 pupae and 0.6 egg masses per three branch samples. The 1993 survey failed to detect any current life stages.

Sample Tree Summary

Two-hundred ninety-one host sample trees were rated for defoliation and monitored for

Table 2. Trees per acre condition summary of subalpine fir and Douglas-fir following a Douglas-fir tussock moth outbreak, Baxter Sawmill, Wasatch-Cache National Forest, July 1993. Summary calculated from 13 variable/fixed plot pairs. SAF = subalpine fir, DF = Douglas-fir.

			Defoliation class									
Diameter	Undamaged		Light		Moderate		Heavy		Very heavy		Mortality	
class	SAF	DF	SAF	DF	SAF	DF	SAF	DF	SAF	DF	SAF	DF
0–4.9″	23.1	0.0	138.5	0.0	23.1	0.0	23.1	0.0	0.0	0.0	253.5	0.0
5–8.9″	12.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	29.3	0.0
9–11.9″	2.5	0.0	7.8	0.0	2.5	0.0	2.1	0.0	0.0	0.0	25.0	0.0
12″ +	3.4	12.8	17.9	6.5	2.7	1.0	0.0	0.0	1.3	0.0	2.7	2.2

TABLE 3. Trees per acre condition summary of subalpine fir and Douglas-fir following a Douglas-fir tussock moth outbreak, Amazon Hollow, Wasatch-Cache National Forest, July 1993. Summary calculated from 12 variable/fixed plot pairs. SAF = subalpine fir, DF = Douglas-fir.

			Defoliation class									
Diameter class	Undamaged		Light		Moderate		Heavy		Very heavy		Mortality	
	SAF	DF	SAF	DF	SAF	DF	SAF	DF	SAF	DF	SAF	DF
0–4.9″	500.0	0.0	275.0	0.0	75.0	0.0	0.0	0.0	25.0	0.0	100.0	25.0
5–8.9″	6.8	0.0	13.4	0.0	4.3	0.0	0.0	0.0	0.0	0.0	40.4	0.0
9–11.9″	5.0	0.0	9.5	0.0	3.1	0.0	0.0	0.0	0.0	0.0	23.0	0.0
12″ +	5.7	2.4	5.5	0.4	0.7	0.3	1.2	0.0	1.8	0.0	14.8	1.3

survival (Tables 4, 5). Defoliator-caused mortality was found to increase with the degree of defoliation. In the very heavily defoliated class, 94% of subalpine firs and 100% of Douglas-firs were killed. None of the sample trees in the lightly defoliated class were killed. Incidence of top-kill also increased with degree of defoliation, although trees in the heavily and very heavily defoliated classes were more likely to succumb than exhibit top-kill. This parallels other tussock moth study results, where degree and incidence of top-kill is related to severity of defoliation (Wickman 1978).

Surviving defoliated trees began to recover by 1993 (Tables 4, 5). Average defoliation rating for lightly defoliated subalpine fir in 1992 was 7.7%. In 1993 the same trees had an average rating of 3.9% with no visible defoliation of that year's needles. The other defoliation classes for subalpine fir and Douglas-fir had similar recoveries. Some of the most dramatic recoveries, however, can be partially attributed to the most heavily defoliated trees of their respective classes succumbing and therefore not being rated in 1993.

DISCUSSION

Although Douglas-fir tussock moth had been previously captured in pheromone traps in Utah, the Wasatch-Cache outbreaks are the first to be documented in the state (Tunnock et al. 1985). More significantly, a literature review revealed the Wasatch-Cache outbreaks to be unique in that subalpine fir is apparently the preferred host type. Balch's (1930, 1932) studies are the only that list subalpine fir as a primary host. More recent literature indicates subalpine fir to be secondary to Douglas-fir, white fir, or grand fir (Wickman et al. 1981, Johnson and Lyon 1988). At the Wasatch-Cache outbreaks, subalpine fir appears to be preferred over Douglas-fir. All three study sites are in close proximity to stands where Douglas-fir is the primary overstory component. These Douglas-fir stands experienced little or no visible defoliation. This contrasts to Balch's Jarbidge, NV, site where subalpine fir, limber pine, and quaking aspen "form practically the whole of the forest" (Balch 1932).

Another exception to the tussock moth's preference for Douglas-fir, white fir, or grand fir has been observed in urban areas along the Colorado Front Range. In these cases blue spruce (*Picea pungens* Engelm.) has been the preferred host over white fir and Douglas-fir (D. Leatherman[2], personal communication). In Colorado's native forests Douglas-fir is the principal host.

The defoliation pattern seen on the Wasatch-Cache National Forest outbreaks differed greatly from previously recorded patterns, such as in Oregon's Blue Mountains. Wickman (1978) recommends estimating defoliation "according to the percent of crown totally defoliated from the top down." That technique was abandoned for this study because most needle loss was distributed evenly throughout the crown rather than concentrated at the top. Application of Wickman's method would have misrepresented many trees with significant defoliation by having them rated at $\leq 10\%$ defoliation. In other words, the Wasatch-Cache National Forest outbreaks did not fit the "top down" defoliation pattern observed in other outbreaks (J. Weatherby[3], personal communication).

This study indicates that subalpine fir may be locally more susceptible to tussock moth mortality than either grand fir or Douglas-fir. Despite the difference in percent defoliation

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TABLE 4. Condition of subalpine fir sample trees within tussock moth monitoring plots at Blind Hollow, Baxter Sawmill, and Amazon Hollow, Wasatch-Cache National Forest, July 1993.

Defoliation class[1]	Class limits (% defoliation)	Average 1992 defoliation (% defoliation)	Average 1993 defoliation[2] (% defoliation)	Total no. of trees	Top-kill #	Top-kill %	Mortality #	Mortality %
Undamaged	0.0	0.0	0.0	51	0	0	0	0
Light	1–24	7.7	3.9	71	7	10	0	0
Moderate	25–74	39.5	36.3	31	14	45	3	10
Heavy	75–89	77.5	77.5	9	2	22	5	55
Very heavy	>90	91.3	72.5	63	2	3	59	94

[1]Trees assigned defoliation class based on 1992 defoliation ratings.
[2]Surviving trees from 1992 defoliation class.

TABLE 5. Condition of Douglas-fir sample trees within tussock moth monitoring plots at Blind Hollow, Baxter Sawmill, and Amazon Hollow, Wasatch-Cache National Forest, July 1993.

Defoliation class[1]	Class limits (% defoliation)	Average 1992 defoliation (% defoliation)	Average 1993 defoliation[2] (% defoliation)	Total no. of trees	Top-kill #	Top-kill %	Mortality #	Mortality %
Undamaged	0.0	0.0	0.0	17	0	0	0	0
Light	1–24	6.5	2.0	20	0	0	0	0
Moderate	25–74	40.0	21.7	3	0	0	0	0
Heavy	75–89	80.0	65.0	2	0	0	1	50
Very heavy	>90	95.0	—	3	0	0	3	100

[1]Trees assigned defoliation class based on 1992 defoliation ratings.
[2]Surviving trees from 1992 defoliation class.

estimation techniques, the Wasatch-Cache results can be compared to those of Wickman (1978). At the 90% defoliation level, Wickman found 24% grand fir mortality and 30% Douglas-fir mortality (90% defoliation in Wickman's study means complete defoliation in the top 90% of the live crown). At the Wasatch-Cache outbreaks, 57% of subalpine fir defoliated at 90% were killed (90% defoliation using the methodology of this study means that 90% of the estimated total needle complement was consumed). At the 99% defoliation level, Wickman found that grand fir died at 53% and Douglas-fir at 46%. This compares to 96% mortality on Wasatch-Cache subalpine fir rated at 95% defoliation.

Within the infested study areas, the degree of damage varies greatly from one plot to the next. One plot at Amazon Hollow had all host type defoliator killed, while a plot 100 m distant was only lightly defoliated. Although the very heavily defoliated areas are restricted in size (usually less than 5 ac), the amount of mortality in these pockets is substantial. An area not sampled, at Baxter Sawmill due to salvage logging operations, included over 20 ac where virtually all host type was killed. Many of these areas are bounded by stands of similar composition and density that were only lightly defoliated. In a study of five case histories in Oregon and California, Wickman et al. (1973) found almost one-half of tree mortality occurring in patches coinciding with high moth population centers.

Douglas-fir tussock moth outbreaks typically span two to four years. Moth populations develop rapidly and then abruptly subside after only one to two years of outbreak populations (Wickman et al. 1981). The Wasatch-Cache outbreaks have followed this pattern. Moderate to heavy defoliation at Baxter Sawmill was first detected from aerial survey in 1990; defoliation was very heavy in 1991. In 1992 moth activity dramatically declined, and in 1993 no life stages were discovered by either visual inspection or pheromone trapping.

While it is beyond this study's scope to identify causal agents that initiated the Wasatch-Cache outbreaks, it should be noted that a prolonged drought coincided with the infestation. Most damage occurred on drier sites, such as ridge tops and southerly facing slopes.

This corresponds to patterns seen in other outbreaks (Bergstrom 1980). The affected trees were apparently drought stressed at the time of defoliation. The sudden moth population collapse mimics that of other outbreaks where a nuclear polyhedrosis virus appears to be the major mortality factor (Wickman et al. 1973).

CONCLUSION

Although uncommon, Douglas-fir tussock moth can cause considerable damage to subalpine fir. While damage in the three study areas was variable, pockets of heavy defoliation had substantial subalpine fir mortality. Larger-diameter trees are apparently less susceptible to mortality except in these pockets where virtually all host type was killed. Although a minor component in the heavily defoliated areas, locally Douglas-fir appears to be less-preferred host material. All study areas are in close proximity to Douglas-fir stands that exhibited little or no tussock moth activity. Western balsam bark beetle and annosus root disease contributed to subalpine fir mortality, though visibly minor relative to defoliator impacts. While forecasting losses in volume would be difficult based on this study, the fate of individual trees can be reasonably predicted given degree of defoliation.

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SEASONAL NUTRIENT CYCLING IN *POTAMOGETON PECTINATUS* OF THE LOWER PROVO RIVER

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ABSTRACT.—A common submersed aquatic plant of Great Basin wetland and riverine systems, *Potamogeton pectinatus* L. (sago pondweed) is a key waterfowl food. Nutritional qualities of submersed aquatics in the Great Basin are little understood. The purpose of this study was to determine the seasonal element cycling and nutritional qualities of *P. pectinatus* drupelet, leaf, and root tissues from the lower Provo River. Leaf tissue protein was 27% (dry weight) in July, but declined to 15% by December. Drupelet protein content was 9% in July and 6.5% in October. Lignocellulose in leaf tissue was lowest in July at 34% and increased as the season progressed. Percent fat was highest in leaf tissue at 12% in July. Sugars were highest in *P. pectinatus* leaf tissues in December and July. Calcium and magnesium concentrations increased in *P. pectinatus* tissues over the entire season. Leaf tissue zinc was 329 ppm (dry weight) in October. Leaf iron concentration was highest in September at 1184 ppm, while root tissue iron was 7166 ppm. Manganese content in leaf tissue peaked in October at 4990 ppm. Copper concentrations in leaves and roots were variable. High protein in leaf tissue would benefit local nesting and brooding waterfowl populations that feed on this aquatic. Trace metal concentrations in leaf and root tissues, from possible anthropogenic activities, appear very high during fall migratory months. Metal bioaccumulation by this species in other Great Basin wetlands and possible metal toxicity in waterfowl warrant further study.

Key words: sago pondweed, Potamogeton pectinatus, *nutritional qualities, trace element cycling, metal bioaccumulation, waterfowl.*

A common submersed aquatic plant of the Great Basin, *Potamogeton pectinatus* is a key primary producer in fresh and saline wetlands (Kantrud 1990). Waterfowl feed on all plant parts including drupelet, leaf, and root tissues (Anderson and Ohmart 1988, Korschgen et al. 1988). Sherwood (1960) noted that whistling swans (*Olor columbianus*) fed heavily on tubers and drupelets during fall migration in the Bear River Migratory Bird Refuge and Ogden Bay Refuge. Other waterfowl species—Canada geese (*Branta canadensis*), mallards (*Anas platyrhynchos*), pintails (*Anas acuta*), gadwalls (*Anas strepera*), canvasbacks (*Aytha vallisneria*), and redheads (*Aytha americana*)—also fed on *P. pectinatus* leaf and root tissues. Localized intermountain trumpeter swan (*Cygnus buccinator*) populations are also largely dependent on submersed aquatic plants as food (Anderson et al. 1986, Henson and Cooper 1993).

Little is known concerning nutrient dynamics and seasonal element cycling of *P. pectinatus* from Great Basin wetlands (Kadlec and Smith 1989). Consequently, how this aquatic species may affect waterfowl nutrition is poorly understood. Most assumptions concerning body condition and nutritional requirements are based on studies from other areas of North America. Yet, energy and sustenance required by waterfowl species that frequent the Great Basin are largely provided by resident aquatic plants. Of these, *P. pectinatus*, *Ruppia maritima* L. (widgeon grass), *Scirpus maritimus* L. (alkali bulrush), *Scirpus pungens* L. (Olney three-square), *Scirpus acutus* L. (hardstem bulrush), and *Zannichellia palustris* L. (horned pondweed) are common plant species managed in national refuges and waterfowl management areas. *Potamogeton pectinatus* is considered the most important of these species for diving and dabbling ducks (Kadlec and Smith 1989). The purpose of this study was to determine the seasonal element concentrations and nutritional qualities of *P. pectinatus* from a local Great Basin river drainage.

METHODS

Plant harvests were conducted monthly from three locations within the lower Provo River drainage from July 1991 to December 1991: (1) just below Deer Creek dam (40°24′N,

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TABLE 1. A range of measured water column and sediment characteristics, pH, and electrical conductivity (EC) from the lower Provo River drainage.

	Water	Sediment
Clarity	clear–opaque	. . .
Velocity (m/sec)	0–0.4	. . .
Depth (cm)	5–60	>120
Temperature (°C)	3–14	3–12
pH	7.4	6.9
EC (μmhos/cm^3)	425	1570

TABLE 2. Mean exchangeable Fe and Mn from lower Provo River drainage sediments (ppm dry weight ± S.E., $n > 3$). Means sharing the same letter are not significantly different ($P \leq .05$).

Depth (cm)	Fe	Mn
0–7	61.6 ± 0.7a	19.2 ± 1.2a
7–15	56.5 ± 1.4a	11.4 ± 0.8b
15–22	61.3 ± 1.7a	9.4 ± 2.1b
22–30	57.1 ± 0.8a	12.0 ± 1.7b

111°31′W, elev. 1603 m), (2) near the Sundance turnoff (40° 22′N, 111°34′W, elev. 1560 m), (3) ≈200 m from the mouth of the Provo River near Utah Lake (40°14′N, 111°44′W, elev. 1347 m). Water column and sediment characteristics measured in the lower Provo River are found in Table 1. Sediment conditions ranged from stony with gravelly patches to silty-clay mud. Stands of *P. pectinatus* were most abundant on muddy sediments.

Whole plants (leaf and root tissues) of *P. pectinatus* were sampled in replicate from each location. Drupelets, shoot (stems and leaves) tissues, and belowground (root, rhizomes, and turions) tissues were separated from plant litter and sediments. Invertebrates were removed from samples when rinsed in warm water (38°C). Cleaned samples were rinsed in deionized water and dried in a forced-air oven at 70°C. Plant, sediment, and water samples were analyzed at Brigham Young University, Department of Agronomy and Horticulture, Plant and Soil Analysis Laboratory. Dry plant tissue samples were weighed and ground in a Wiley Mill to pass a 40-mesh screen, and 0.25-g samples were digested in Folin-Wu tubes with 5 ml of concentrated HNO_3. Samples were left covered for 16 h before digestion in an aluminum block for 1 h at 100°C. Three ml of 70% $HClO_4$ was added, and samples were refluxed at 200°C until the solution cleared (approx. 30 min). Samples were then brought to 50-ml volume with deionized water (Orson et al. 1992). Element contents were detected by direct aspiration into a Perkin-Elmer Model 5000 Atomic Absorption Spectrophotometer. All blanks and standards were run with the same procedures. Percent total nitrogen and phosphorus were determined using a Kjeldahl digestion followed by analysis with an ALP-KEM rapid-flow analyzer.

Sediment (0–30 cm) and water (1000 ml) samples were obtained from the same locations and intervals as plant samples. Sediments were air-dried and extracted for exchangeable iron (Fe) and manganese (Mn) with diethylenetriaminepenta-acetic acid (DTPA) and detected by atomic absorption spectroscopy. Water samples were analyzed for pH, electrical conductivity (μmhos/cm^3), and available Fe and Mn with an Orion Microprocessor Ion-analyzer/901 pH meter, a wheatstone bridge, and by atomic absorption spectroscopy.

Mean concentrations and standard errors (S.E.) were determined for each plant, sediment, and water sample. To determine if significant variation in plant tissue nutrient and element concentrations existed between the different months, we used analysis of variance (ANOVA) where month was considered the fixed effect and sample site the experimental unit in a repeated measures design. If significance ($P \leq .05$) was found, Tukey's multiple comparison procedures were used to separate means.

RESULTS AND DISCUSSION

Available Fe and Mn concentrations in water samples were 0.06 ± 0.01 and 0.001 ppm. Sediment exchangeable Fe and Mn contents were found between the normal soil range of 5–65 ppm. Yet, under anoxic conditions that are common in sediments, Fe and Mn may become more available for root uptake (Spencer and Brewer 1971, Tisdale et al. 1985; Table 2). Significant differences in sediment exchangeable Mn were found between surface sediments (0–7 cm) and the rest of the sampled profile (Table 2).

Element concentrations and forage qualities were determined for *P. pectinatus* tissues from July to December. Leaf and root tissue dry matter, as a percentage of fresh weight, remained constant at 6–7%, with the highest dry matter content observed in October. Throughout the season, *P. pectinatus* element and forage composition varied with growth stage. Significant variation in leaf tissue protein was found (F = 21.69; d.f. = 4,14; $P <$ .001) between July, September, October, and December (Table 3). Drupelet protein content was higher in July than in October. In all months sampled, leaf tissue protein was higher than drupelet protein. Percent protein in leaf tissue was higher than values reported in other studies (Linn et al. 1975, Kantrud 1990). Acid detergent fiber (ADF) analysis revealed that leaf tissue was lowest in lignocellulose (fiber) in July, but significant differences (F = 3.03; d.f. = 4,14; $P =$ .07) in fiber content were not observed as the year progressed. Linn et al. (1975) found *P. pectinatus* leaf fiber content of 33% that is similar to values observed in this study. Increased fiber content would decrease the overall forage quality of leaf tissue. Significant variation did exist (F = 177.40; d.f. = 4,14; $P <$ .001) in leaf tissue fat content and was highest in July. Total nonstructural carbohydrates (sugars) in leaf tissues were highest in December and differed from all other months (F = 42.19; d.f. = 4,14; $P <$ .001). By October, drupelet fat and sugar content were both higher than values found in July.

Percent nitrogen (N) and phosphorus (P) in leaf tissue reached peak concentrations in July but were significantly lower by December (F = 23.37; d.f. = 4,14; $P <$ .001) (F = 79.30; d.f. = 4,14; $P <$ .001; Table 4). Vermaak et al. (1983) stated that *P. pectinatus* played an important role in P cycling in aquatic systems. Cultured *P. pectinatus* grown in water relatively high in phosphate (PO_4–P) (0.3 ppm) bioaccumulated P^{32} to 4738 times the amount found in the water column. Nitrogen and P content in *P. pectinatus* can be well above that required for plant growth; this would indicate luxury consumption of these elements (Jupp and Spencer 1977, Ho 1979, Madsen 1986). Significant concentrations of calcium (Ca) and magnesium (Mg) accumulated (F = 29.12; d.f. = 4,14; $P <$ .001) (F = 278.71; d.f. = 4,14; $P <$ .001) in leaf tissue between July and December. This may indicate abiotic deposition, though no visible encrustation on exterior leaf or stem surfaces was observed. Hutchinson (1975) reported that *P. pectinatus* leaves were higher in Ca, Fe, K, Mg, Na, and several micronutrients than other aquatic plants. Yet, no mention of time sampled was given for these mineral concentrations. Therefore, no knowledge of seasonal accumulation was determined. Potassium (K) content was highest in September and differed significantly from percent K content in July (F

TABLE 3. Mean protein, fiber, fat, and sugar content in *P. pectinatus* drupelet and leaf tissue over five months. Forage quality constituents expressed as % dry weight ± S.E., $n > 3$. Means sharing the same letter are not significantly different ($P \leq .05$).

Month	Tissue	Protein	ADF[a]	Fat	TNC[b]
		(% dry wt.)			
July	Leaf	27.4 ± 0.3a	34.2 ± 0.9a	12.2 ± 0.1a	8.3 ± 0.1a
Aug.	Leaf	24.9 ± 0.3ab	35.6 ± 2.8a	6.5 ± 0.2b	8.1 ± 0.4a
Sept.	Leaf	21.4 ± 0.3b	39.7 ± 0.4a	6.8 ± 0.2b	7.9 ± 0.2a
Oct.	Leaf	20.3 ± 1.4b	37.9 ± 1.3a	7.1 ± 1.1b	8.6 ± 0.1a
Dec.	Leaf	15.1 ± 0.3c	38.1 ± 0.5a	5.9 ± 1.1c	11.0 ± 0.1b
July	Drupelet	9.0 ± 0.5	33.4 ± 0.6	6.1 ± 0.7	12.0 ± 0.3
Oct.	Drupelet	6.5 ± 0.8	36.3 ± 1.3	7.4 ± 0.8	16.3 ± 1.2

[a] Acid detergent fiber (ADF), a measure of percent lignocellulose or fiber
[b] Total nonstructural carbohydrate (TNC), a measure of sugars

TABLE 4. Mean mineral element concentration in *P. pectinatus* leaf tissue over five months. Element content expressed as % dry weight ± S.E., $n > 3$. Means sharing the same letter are not significantly different ($P \leq .05$).

Month	Tissue	N	P	K	Ca	Mg	S
		(% dry wt.)					
July	Leaf	4.4 ± 0.7a	0.6 ± 0.1a	1.9 ± 0.2a	1.3 ± 0.1a	0.3 ± 0.04a	1.2 ± 0.1a
Aug.	Leaf	2.8 ± 1.0a	0.5 ± 0.1a	3.5 ± 0.1b	1.2 ± 0.1a	0.5 ± 0.01b	
Sept.	Leaf	3.4 ± 0.1a	0.5 ± 0.2a	3.7 ± 0.1b	1.4 ± 0.04ab	0.6 ± 0.02c	1.8 ± 0.2b
Oct.	Leaf	3.3 ± 0.2a	0.5 ± 0.1a	3.1 ± 0.1b	1.7 ± 0.1b	0.6 ± 0.01c	
Dec.	Leaf	2.4 ± 0.1b	0.2 ± 0.1b	3.0 ± 0.3b	2.3 ± 0.1c	0.7 ± 0.02c	0.6 ± 0.1c

TABLE 5. Mean trace element concentration in *P. pectinatus* leaf tissue over five months. Element content expressed as ppm dry weight ± S.E., $n > 3$. Means sharing the same letter are not significantly different ($P \leq .05$).

Month	Tissue	Zn	Fe	Mn	Cu
		(ppm dry wt.)			
July	Leaf	213 ± 14a	633 ± 67a	122 ± 6a	21 ± 4a
Aug.	Leaf	185 ± 10a	1097 ± 58b	1744 ± 101b	10 ± 1b
Sept.	Leaf	211 ± 1a	1184 ± 75b	3861 ± 117c	10 ± 1b
Oct.	Leaf	329 ± 4b	963 ± 73b	4990 ± 48d	11 ± 0b
Dec.	Leaf	295 ± 13b	1038 ± 63b	2130 ± 65b	8 ± 0b

= 26.40; d.f. = 4,14; $P < .001$). Percent sulfur decreased between July and December ($F = 13.41$; d.f. = 2,10; $P = .03$; Table 4).

Zinc (Zn) concentration in leaf tissue was significantly higher ($F = 36.56$; d.f. = 4,14; $P < .001$) in October and December than in all other months (Table 5). Mean Fe content was higher in August leaf tissue than in July ($F = 12.59$; d.f. = 4,14; $P = .001$), after which Fe content remained fairly constant throughout the remainder of the sample period. Leaf tissue Mn content increased through the season and was highest in October ($F = 587.38$; d.f. = 4,14; $P < .001$; Table 5). Dudkin et al. (1976) found that *P. pectinatus*, growing in polluted coastal waters of the Black Sea, accumulated Mn to 0.5% (dry weight). This Mn concentration corresponds to values found in this study. Yet, Mn concentrations in water and sediment from the lower Provo River appear normal. Copper (Cu) in leaf tissue varied significantly ($F = 44.48$; d.f. = 4,14; $P < .001$), with high concentrations in July followed by lows in August through December (Table 5).

Root tissues (root, rhizomes, and turions) of *P. pectinatus* were not separated for analysis. Mean root tissue forage qualities, compared to leaf tissues, were lower in percent protein but higher in fat content (Table 6). Phosphorus was the only mineral element with a concentration higher in root tissues than in leaf tissues. Mineral (N, P, K, Ca, and Mg) contents of root tissues in this study were similar to contents found in other studies (Kollman and Wali 1976, Van Vierssen 1982). High trace metal concentrations were also found in root tissues. Like leaf tissues, mean Fe and Mn concentrations in root tissues appear inordinately high.

CONCLUSIONS AND FUTURE RESEARCH

Seasonal variation did exist in forage qualities and nutrient concentrations in *P. pectinatus*. Protein content in leaf tissue was highest in the summer months when *P. pectinatus* was growing rapidly. By fall and early winter, protein content decreased but was still higher than concentrations found in drupelets. Apparently, protein content in *P. pectinatus* leaf tissue from the lower Provo River was higher than concentrations reported elsewhere. High protein content in leaves and stems in the summer months would greatly benefit nesting and brooding waterfowl that feed on this aquatic species. Drupelet fat and sugar content was higher than that for leaf or root tissues in October. This would tend to confirm why drupelets are so eagerly sought after by staging and migrating waterfowl. Trace metal (Fe and Mn) contents in leaf and root tissues accumulated over the season and were very high by fall. However, water and sediment concentrations appear normal. It should be determined whether the trace metal concentrations observed are of natural or anthropogenic origin. Future research should develop a greater understanding of heavy metal accumulation in this and other key Great Basin aquatic plant species.

TABLE 6. Forage quality, mineral and trace element concentration of *P. pectinatus* root tissue (root, rhizome, and turions) averaged over five months. Forage quality constituents and mineral content expressed as % and ppm dry weight ± S.E., $n > 3$.

Protein	ADF	Fat	TNC[a]
(% dry wt.)			
13.0 ± 1.0	nd[b]	10.9 ± 3.0	11.9 ± 1.3

N	P	K	Ca	Mg
(% dry wt.)				
2.1 ± 0.2	0.4 ± 0.1	2.9 ± 0.2	1.5 ± 0.2	0.3 ± 0.1

Zn	Fe	Mn	Cu
(ppm dry wt.)			
167 ± 25	7166 ± 1438	2051 ± 570	14.8 ± 3.3

[a] Total nonstructural carbohydrate (TNC), a measure of sugars

[b] Not determined

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FACTORS INFLUENCING FISH ASSEMBLAGES OF A HIGH-ELEVATION DESERT STREAM SYSTEM IN WYOMING

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ABSTRACT.—Seven fish species were found in the Bitter Creek drainage of southwest Wyoming, but only speckled dace (*Rhinichthys osculus*), flannelmouth sucker (*Catostomus latipinnis*), and mountain sucker (*Catostomus platyrhynchus*) were indigenous. No relationships were found between fish standing stocks and habitat features, but species richness was related to elevation and stream width. No fish were found above an elevation of 2192 m. Only the most downstream study reach had more than three species present. Two indigenous species, speckled dace and mountain sucker, and a nonnative species, fathead minnow (*Pimephales promelas*), were predominant fishes in the drainage. These three species withstand intermittent stream flows that are common in the drainage.

Key words: fish, streams, desert, Wyoming, habitat, distribution.

Fish communities in streams become more complex as habitat diversity increases along the length of a stream. Variation in fish community structure within a stream system can follow patterns of zonation or addition. Specific fish communities can be associated with zones defined by water temperature or geomorphologic features, or community complexity can increase with progression downstream by addition of species (Moyle and Nichols 1973, Guillory 1982, McNeely 1986, Hughes and Gammon 1987, Platania 1991, Rahel and Hubert 1991). However, such patterns may differ in arid drainages of the western United States with depauperate ichthyofauna (Cross 1985).

Little is known about the fish communities in high-desert stream systems in southwestern Wyoming. Annual precipitation over most of these drainages is <16 cm, with much of it as snow in headwater areas during late winter and thunderstorms during late summer. Discharge is highest during spring runoff, and streams frequently become intermittent during summer and winter. Because these systems in Wyoming are at high elevations (>1800 m above mean sea level), water temperatures are cool compared with other desert streams. The climate in these areas typically consists of dry, moderately warm summers with long, cold winters.

The purpose of this study was to (1) describe fish species present in a high-desert stream system in southwestern Wyoming and (2) determine the factors that influence fish abundance and community structure within the drainage.

STUDY AREA

The study was conducted in an intermittent drainage, Bitter Creek, a tributary to the Green River in the Red Desert of southwest Wyoming (Fig. 1). The study area consists of Bitter Creek and four tributaries—Little Bitter, Salt Wells, Bean Springs, and Gap creeks. Frequently, no measurable surface flow occurs in Bitter Creek at Bitter Creek, WY, during midsummer and midwinter (flow data available in the Water Resources Data System at the Wyoming Water Resources Center, University of Wyoming, Laramie). Bitter Creek at Salt Wells, WY, generally has no measurable surface flow from July to February. Salt Wells Creek has more persistent flows near its mouth, but records of no measurable flows occur in midsummer and midwinter. When no measurable flow occurs in these streams, isolated pools of standing water can be found in the stream channels. Elevation of the study area ranges from 1800 to 2400 m.

Streams in the Bitter Creek drainage typically are downcut by at least 1.5 m, with steep clay banks having no vegetation. Riparian vegetation consists of grasses and sagebrush (*Artemisia* spp.); upland vegetation is primarily the latter.

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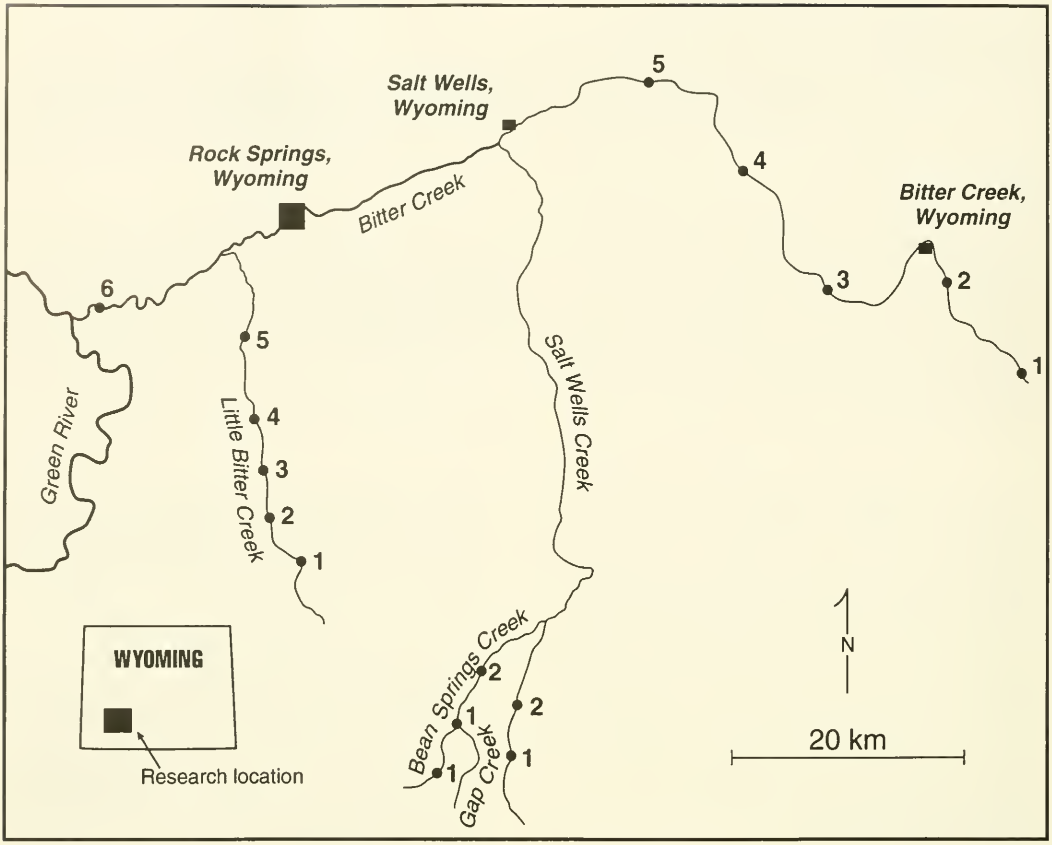
Salt Wells, Wyoming
Rock Springs, Wyoming
Bitter Creek
Bitter Creek, Wyoming
5
4
3
2
1
6
5
4
3
2
1
Green River
Little Bitter Creek
Salt Wells Creek
Bean Springs Creek
Gap Creek
2
1
1
2
1
N
20 km
WYOMING
Research location

Fig. 1. Map of the Bitter Creek drainage, WY, showing the location of the 16 study reaches.

Baxter and Simon (1970) reported four fish species in collections at two sites in Bitter Creek. Speckled dace (*Rhinichthys osculus*), fathead minnow (*Pimephales promelas*), and mountain sucker (*Catostomus platyrhynchus*) were reported from a site about 10 km upstream from the mouth. Bluehead sucker (*Catostomus discobolus*) was the only species reported from a site near Salt Wells.

METHODS

Sixteen 100-m-long study reaches were selected to represent variation in stream size and habitat in the drainage during summer 1993. Wetted width, mean depth, and substrate were determined across transects at 10-m intervals. Dominant substrate at each transect was visually determined following Bain et al. (1985): sand-silt (<2 mm diameter), gravel (2–16 mm), pebble (17–64 mm), cobble (65–256 mm), and boulder (>256 mm). Water velocity was determined within each reach using the dye flow method (Binns 1982). Stream discharge at time of sampling was computed from width, depth, and velocity.

Alkalinity, hardness, and pH were measured at the time of sampling. Alkalinity and hardness were determined with field test kits (Hach Model A1-36DT), pH with an electronic meter. Mean elevation and channel slope at each study reach were estimated from 7.5-minute topographic maps.

Fish were sampled in each 100-m reach by electrofishing. Small-mesh (6.4-mm) block nets were placed at each end, and two or three electrofishing passes were made over the entire reach. Three-pass depletion estimates of species abundance were made in most reaches. Two-pass depletion estimates were used when >80% of fish captured by the first two passes were captured during the first pass. Fish abundance was computed using the Zippin method (Platts et al. 1983). All fish were weighed to enable computation of standing stock estimates.

Standing stocks of individual species, total standing stock of all species, and number of species in a reach were evaluated for their relation to nine habitat variables using simple-linear and multiple-regression analyses. Independent variables were included in regression models if they were significant at $P \leq .05$. We further limited inclusion of dependent variables in multiple-regression models to ones that were not correlated at $P \leq .05$. Computations were performed using Statistix 4.0 (Analytical Software 1992).

RESULTS

Seven fish species were collected: speckled dace, fathead minnow, Utah chub (*Gila atraria*), Bonneville redside shiner (*Richardsonius balteatus hydrophlox*), mountain sucker, white sucker (*Catostomus commersoni*), and flannelmouth sucker (*C. latipinnis*). Abundance varied substantially among study reaches (Table 1). Mean total standing stock of all species was 3.0 g/m^3 and ranged from 0 to 21.3 g/m^3. No fish were found in the four reaches above 2192 m.

Habitat features varied among the 16 study reaches (Table 2). Flow was measurable at all reaches. Stream width, water velocity, and discharge increased downstream. Sand-silt substrate occurred over >90% of almost all study reaches. Alkalinity, pH, and hardness also increased downstream.

No significant relations were found between any of the nine habitat variables and standing stocks of individual species or total standing stock of all species. However, there were significant relations between the number of species and four habitat variables:

$$NS = 20.88 - 0.0091\ E\ (P = .0003,\ R^2 = .61),$$
$$NS = 0.13 + 0.812\ W\ (P = .0010,\ R^2 = .52),$$
$$NS = 3.40 - 11.008\ V\ (P = .029,\ R^2 = .33),\ \text{and}$$
$$NS = 0.57 + 31.245\ F\ (P = .022,\ R^2 = .32),$$

where NS = number of species, E = elevation in meters, W = mean wetted width in meters, V = water velocity in meters per second, and F = flow in cubic meters per second. The best two-variable model was

$$NS = 14.36 - 0.0065\ E + 0.53\ W\ (P < .0001,\ R^2 = .80).$$

As study reaches declined in elevation and as width, water velocity, and discharge increased, the number of species increased.

Because the most downstream reach on Bitter Creek had twice as many species as any other reach and flow at the reach was enhanced by discharge from a sewage treatment plant, we assessed relations with the omission of that reach. Again, no relationships were found between any of the habitat variables and standing stocks of fish, but the number of species (NS) was significantly related to elevation (E) and water velocity (V):

$$NS = 15.95 - 0.0068\ E\ (P = .0014,\ R^2 = .55),\ \text{and}$$
$$NS = 3.00 - 10.11\ V\ (P = .0018,\ R^2 = .51).$$

Among the 15 study reaches with a maximum of three species present, the number of species increased with decline in elevation and water velocity.

DISCUSSION

Of the seven fish species in the Bitter Creek drainage, only three—speckled dace, flannelmouth sucker, and mountain sucker—are indigenous (Baxter and Simon 1970). Absence of fish above 2192 m is probably due to a climate that is too cold for warmwater fishes. Additionally, no trout occur naturally or have become naturalized in the watershed.

The number of species increased with progression from headwater to downstream reaches (Table 1). With the exception of the most downstream reach on Bitter Creek, no more than three species—specked dace, mountain sucker, and fathead minnow—were found in any of the study reaches. The high-elevation reaches with fish tended to have predominantly or exclusively speckled dace and mountain sucker.

Much of the increase in species richness with downstream progression was due to the most downstream reach on Bitter Creek where six species were found (Table 1). Four of six species were not natives—fathead minnow, white sucker, Utah chub, and Bonneville redside shiner. Mountain sucker was not found in this reach, but it was common throughout most of the Bitter Creek drainage. While this study reach was lowest in elevation among the 16 study reaches, it also was downstream from the outfall of the wastewater treatment facility

TABLE 1. Standing stocks (g per m^2) of fishes at 16 study reaches in the Bitter Creek drainage, WY, sampled during summer 1993.

	Bitter Creek						Little Bitter Creek					Salt Wells Creek		Beans Spring	Gap Creek	
Species	1	2	3	4	5	6	1	2	3	4	5	1	2	1	1	2
Speckled dace	2.5	1.1	0.8	<0.1	0.5	<0.1			0.2	0.4	0.4				5.7	0.2
Mountain sucker	1.7	<0.1	2.3		0.4				5.8	1.8	0.2				15.6	
Fathead minnow						<0.1		2.9	0.5	0.4						0.5
Flannelmouth sucker						2.4										
White sucker						2.2										
Utah chub						<0.1										
Bonneville redside shiner						<0.1										
Total	4.2	1.2	3.1	<0.1	1.0	4.7			6.5	2.6	0.6				21.3	0.7

TABLE 2. Habitat features at 16 study reaches in the Bitter Creek drainage, WY, sampled during summer 1993.

Habitat	Bitter Creek						Little Bitter Creek					Salt Wells Creek		Beans Spring	Gap Creek	
feature	1	2	3	4	5	6	1	2	3	4	5	1	2	1	1	2
Mean wetted width (m)	1.3	1.9	2.7	1.2	1.8	7.2	2.0	1.4	2.4	2.1	1.3	1.2	2.1	0.8	1.3	1.3
Mean water depth (m)	0.14	0.13	0.26	0.21	0.15	0.14	0.08	0.09	0.20	0.09	0.18	0.13	0.09	0.12	0.12	0.21
Water velocity (m/second)	0.10	0.16	0.09	0.07	0.06	0.13	0.13	0.27	0.12	0.13	0.05	0.32	0.27	0.25	0.14	0.11
Discharge (m^3/second)	0.02	0.04	0.06	0.02	0.01	0.13	0.02	0.03	0.06	0.02	0.01	0.05	0.05	0.02	0.02	0.03
Channel slope (%)	0.2	0.3	0.1	0.2	0.1	0.1	2.1	1.1	0.8	0.7	0.4	2.8	2.8	1.4	2.1	0.5
Elevation (m × 1000)	2.10	2.06	2.02	2.00	1.98	1.88	2.33	2.12	2.06	2.04	1.96	2.38	2.29	2.29	2.18	2.09
Alkalinity (mg/L × 100)	2.6	2.8	2.6	2.5	2.7	3.8	2.0	3.0	2.6	2.9	3.3	2.4	3.8	2.2	2.2	2.2
Hardness (mg/L × 100)	1.9	1.7	2.0	2.1	3.2	9.5	2.6	5.2	4.6	4.8	14.5	2.8	7.6	3.4	3.5	4.6
pH	6.6	9.3	7.9	8.0	7.2	8.7	7.0	7.6	8.1	8.5	7.7	8.5	7.9	8.0	7.8	9.5

for Rock Springs, WY, and was only 13 km upstream from the confluence of Bitter Creek and the Green River. The more permanent flows due to the wastewater treatment facility may have enabled fish not adapted to intermittent flows to persist in this reach. Also, the relatively short distance to the Green River may enable upstream migration of fish to this reach, contributing to higher species diversity. Repeated invasion of nonnative species from downstream reservoirs maintains species diversity in the Virgin River, UT (Cross 1985). Also, human disturbances have been found to create environmental conditions favorable to nonnative fish in California (Moyle and Nichols 1973, 1974). Therefore, enhanced flows due to the wastewater treatment facility and invasion of nonnative species from the Green River probably contribute to the diversity of fish in the downstream portion of Bitter Creek.

During summer 1993, flowing water occurred at all study reaches when they were sampled. Precipitation in spring and summer 1993 was substantially greater than normal, enabling measurable surface flows to persist during summer. However, study reaches upstream from the outfall of the Rock Springs, WY, wastewater treatment facility are frequently intermittent during late summer. Fathead minnow has been described previously as a species associated with intermittent streams (Baxter and Simon 1970, Pflieger 1975). Our observations indicate that two indigenous species—speckled dace and mountain sucker—and one introduced species—fathead minnow—can survive in the frequently intermittent streams. Consequently, these three fishes are the only species occurring over most of the Bitter Creek drainage, but fathead minnows tend to be limited to lower elevations than the two native species. It is not known how the invasion by fathead minnow may affect the native speckled dace and mountain sucker in this desert stream system.

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SPECIATION BY ANEUPLOIDY AND POLYPLOIDY IN *MIMULUS* (SCROPHULARIACEAE)[1]

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Key words: Mimulus, *speciation, evolution, aneuploidy, polyploidy.*

Speciation by aneuploid and polyploid changes in chromosome numbers is so common in flowering plants as to be almost a characteristic of the angiosperms. Elegant examples of these patterns of evolution are exhibited by monkey flowers of the genus *Mimulus* (Scrophulariaceae).

The genus *Mimulus* contains some 150 species occurring in western North and South America with a few outlying species in eastern North America, Japan, Vietnam, the Himalayas, New Zealand, Australia, and South Africa. The center of diversity is California, with a secondary center in Chile. Some species are annuals of deserts, grasslands, or forests; some are biennials of marshy places; some are herbaceous perennials from springs, streamsides, or lake-shore habitats; and others are woody shrubs of the dry California chaparral. The species form clusters reflecting these various life forms. There are 8–10 such clusters commonly recognized as sections of the genus *Mimulus* (Grant 1924, Pennell 1951, Chuang and Heckard personal communication).

Chromosome numbers of over 50 species (Table 1), that is, approximately one-third of the *Mimulus* species, have been ascertained by Vickery and his co-workers (Vickery 1978, Vickery, Chu et al. 1981, Vickery, Simpson et al. 1981, Vickery et al. 1982, 1985, 1986, 1990, unpublished) and by Chuang and Heckard (personal communication). Chromosome numbers reveal intriguing patterns of evolution by aneuploidy and polyploidy.

First, let us consider the base chromosome numbers of the eight main sections of the genus. Section *Mimulastrum* has a base number of $x = 7$; *Eunanus* and *Erythranthe* have base numbers of $x = 8$; *Paradanthus* 8, 9, 10; *Eumimulus* 8, 11, 12; *Oenoe* 9; *Diplacus* 10; and *Simiolus* 14, 15, 16, 30. Base numbers of the sections suggest extensive evolution by both aneuploidy and polyploidy. For the genus as a whole, the base number appears to be $x = 8$, inasmuch as the other plausible base number, $x = 7$, is found only in one, apparently derived, desert species, *M. mohavensis* Lemmon (Table 1).

Next, let us consider the chromosome numbers by individual species. All species counted thus far are the same in each of several sections, specifically, in *Mimulastrum*, *Erythranthe*, *Oenoe*, and *Diplacus*. The other sections are polymorphic for their species' chromosome numbers and frequently exhibit speciation by aneuploidy and/or polyploidy, often in complex combinations. For example, the various species of section *Eumimulus* exhibit $n = 8$, 11, and 12; species of section *Eunanus* exhibit $n = 8$, 10, and 16; species of section *Paradanthus* exhibit $n = 8$, 9, 16, 17, 18, and 30; and species of section *Simiolus* exhibit $n = 13$, 14, 15, 16, 24, 28, 30, 31, 32, 46, and 48 (Table 1).

Section *Simiolus*, which shows by far the most speciation by aneuploidy and/or polyploidy of all sections of the genus, consists of six species groups, that is, complexes of related species and varieties. First is the *M. guttatus* complex, centered in California; it has as its base number $x = 14$, with aneuploid forms at $n = 13$ and $n = 15$ (Table 1), as well as tetraploid forms with $n = 28$. Second is the alpine (western United States) *M. tilingii* complex with its base number of $x = 14$ and aneuploid forms at $n = 15$, $n = 16$, and an unusual polyploid form at $n = 24$. The third species group is the *M. dentilobus* complex of southwestern United States and northwestern Mexico with its base number of $x = 16$ and an aneuploid form at $n = 15$. Fourth is the *M. luteus* complex

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[1] A talk presented 4 September 1993 as part of the symposium, "Plant Evolution," at the National Institute of Genetics, Mishima, Japan.

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TABLE 1. Chromosome numbers in the genus *Mimulus* by sections (counts by Chuang and Heckard and by Vickery and co-workers; see text for references).

Taxon	n =
Mimulastrum Gray (x = 7)	
M. mohavensis Lemmon	7
Eunimulus Gray (x = 8, 11, 12)	
M. alatus Aiton	11
M. gracilis R. Br.	8
M. ringens L.	8, 12
Eunanus Gray (x = 8)	
M. bolanderi Gray	8
M. layneae (Greene) Jepson	8
M. brevipes Bentham	8
M. cusickii (Greene) Piper	8
M. nanus Hook. & Arn.	8
M. torreyi Gray	10
M. biglovii Gray	16
Paradanthus Grant (x = 8, 9, 10)	
M. bicolor Hartweg ex Bentham	8
M. filicaulis Watson	8
M. breweri (Greene) Coville	16
M. floribundus Douglas	16
M. moschatus Douglas	16
M. latidens (Gray) Greene	16
M. arenarius Grant	16
M. primuloides Rydb.	9, 17, 18
M. repens R. Br.	10
M. nepalensis Bentham	16, 30
Erythranthe Greene (x = 8)	
M. cardinalis Douglas	8
M. eastwoodiae Rydb.	8
M. lewisii Pursh	8
M. nelsonii Grant	8
M. rupestris Greene	8
M. verbenaceus Greene	8
Oenoe Gray (x = 9)	
M. pictus (Curran) Gray	9
M. tricolor Lindl.	9
M. pygmaeus Grant	9 (or 10?)
M. pilosellus Greene	9
Diplacus Gray (x = 10)	
M. aridus (Abrams) Grant	10
M. aurantiacus Curt.	10
M. calycinus Eastw.	10
M. clevelandii Brandg.	10
M. fasiculatus (Pennell) McMinn	10
M. longiflorus (Nutt.) Grant	10
M. puniceus (Nutt.) Steud.	10
Simiolus Greene (x = 14, 15, 16)	
M. gutatus Fischer ex DC.	14, 15, 28
M. laciniatus Gray	14
M. nasutus Greene	13, 14
M. glaucescens Greene	14
M. platycalyx Pennell	15
M. tilingii Regel	14, 15, 24, 28
M. gemmiparus Weber	16
M. dentilobus Rob. & Fern.	15, 16
M. wiensii Vickery	16
M. glabratus HBK	15, 30, 31
M. andicolus HBK	46
M. pilosiusculus HBK	46
M. externus (Skotts.) Skotts	46
M. luteus L.	30, 31, 32
M. cupreus Dombrain	31
Undescribed	
n. sp #A	16
n. sp #B	32
n. sp #C	32, 48 ± 1–4

from the central and southern Andes of South America. Its base number is $x = 30$, but there are $n = 31$ and $n = 32$ forms as well. Fifth, there is the *M. glabratus* complex that ranges from Canada to Patagonia. Its varieties in central North America exhibit the base number of the complex, $x = 15$. In the Rio Grande drainage we find tetraploids with $n = 30$. From northern Mexico to southern Colombia we find the aneuploid tetraploid $n = 31$ varieties of the complex. From Ecuador south to southern Argentina and including the Juan Fernandez Islands off the coast of Chile, we find the aneuploid hexaploid species and varieties with $n = 46$ chromosomes. Apparently, each change in chromosome number facilitated an adaptive radiation further south. Last is the *M. wiensii* complex of the mountains of western Mexico with its base number of $x = 16$ and three apparent new species that are morphologically distinct and reproductively isolated (Vickery et al. unpublished). One has $n = 16$ chromosomes, one has $n = 32$ chromosomes, and the third has two forms—one with $n = 32$ chromosomes and the other with $n = 48 \pm 1$–4 chromosomes (incipient aneuploidy?).

How does speciation by aneuploidy and polyploidy occur? We carefully examined meiosis in *M. glabratus* var. *utahensis* and *M. glabratus* var. *fremontii*, two of the widespread diploid varieties of the *M. glabratus* complex, and their intervarietal F_1 hybrids. First, of 1317 cells examined in diakinesis or metaphase of first meiosis (Tai and Vickery 1970, 1972), 1090 exhibited regular 15 bivalent chromosomes. Another 23 cells, or 1.7%, had aneuploid numbers of chromosome pairs ranging from only 6 to as many as 13, plus 4–18 univalents. These cells presumably could produce aneuploid gametes, at least in some cases. A sizeable minority, 204 cells, exhibited 14 II and 2 I, or 13 II and 1 IV, or complement fractionation with its uneven groupings of chromosomes. These cells might produce aneuploid gametes also. Second, of 782 additional cells observed in Anaphase I, 294 (37.5%) exhibited unequal disjunction, laggard chromosomes, or chromatin bridges. These cells also could result in aneuploid gametes. Some 47 of these abnormalities occurred in *M. glabratus* var. *fremontii*, only 18 occurred in *M. glabratus* var. *utahensis*, but most, 229, occurred in the intervarietal hybrids. Thus, varieties differ in their potential for producing aneuploid gametes, and intervarietal hybrids are particularly prone to do so. This suggests to me that natural hybridization probably plays a significant role in evolution in monkey flowers. Finding occasional plants in various populations with aneuploid chromosome numbers indicates that aneuploid gametes not only are produced, but actually function. Third, of 95 cells examined in Anaphase II, 22 were polyploid and could presumably lead to polyploid gametes. Thus, we see significant numbers of the very cytological abnormalities in the basic diploid varieties that could lead to evolution by aneuploidy and polyploidy, that is, to the very patterns of evolution that we actually see in the *M. glabratus* complex.

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SPECIATION IN *MIMULUS*, OR, CAN A SIMPLE FLOWER COLOR MUTANT LEAD TO SPECIES DIVERGENCE?[1]

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Key words: Mimulus, Erythranthe, *speciation, reproductive isolation, flower color mutations, pollinators, bumblebees, hummingbirds.*

The general pattern of speciation in nature has been clear for a long time—the divergence of portions of a population, usually small (Levin 1993), usually in geographic isolation (Mayr 1976), and the accumulation of genetic changes by selection and/or genetic drift (Crow and Kimura 1970) that produce reproductive isolation and normally character divergence as well. The critical step is reproductive isolation, and yet that step—except for polyploid formation which in itself is not always effective (DeWet 1980)—has rarely been observed actually happening in nature. A promising group in which to study speciation events in progress is section *Erythranthe* of the genus *Mimulus* (Vickery 1978).

The six species of monkey flowers comprising section *Erythranthe* are moisture-requiring, herbaceous perennials 1–10 dm in height, with variously shaped, opposite leaves and bilabiate flowers that have four stamens, one style with a bilobed sensitive stigma, and five corolla lobes that range in color from orange to red—rarely yellow—and from lavender-pink to magenta-pink—rarely white. See Grant (1924) for further details. When considered species by species, corollas of *M. cardinalis* Douglas vary from orange to red—rarely yellow—and are sharply and fully reflexed, hummingbird-pollinated flowers. Corollas of *M. verbenaceus* Greene are partially reflexed; that is, the upper two corolla lobes are reflexed, whereas the lower three are gently recurved. Flowers are orange-red to red—rarely yellow—and also are hummingbird-pollinated. Corollas of *M. nelsonii* Grant are partially re-flexed also and have orange-red to red flowers, which are longer than those of *M. verbenaceus* (6–7 cm versus 4–5 cm). Corollas of *M. eastwoodiae* Rydberg and *M. rupestris* Greene, the two cliff-dwelling species, are partially reflexed, red, and typically hummingbird-pollinated also. And last, flowers of the Rocky Mountain variety of *M. lewisii* Pursh are magenta-pink with all five corolla lobes gently recurved rather than reflexed, thus forming a bee-landing platform; flowers of the Sierra Nevada variety of *M. lewisii* are lavender-pink—rarely white—with corolla lobes thrust forward. Both varieties of *M. lewisii* are bee-pollinated. *Mimulus lewisii* flowers and those of *M. eastwoodiae* and *M. rupestris* produce only modest amounts of nectar, whereas the other species produce abundant nectar (Table 1). Thus, the species differ markedly in flower shape, flower color, nectar production, and, consequently, in pollinators servicing the flowers. In the formation of the six species, evolution appears to have responded to selection imposed by pollinator preferences and ecological opportunities. The result is that members of the complex have radiated into a wide variety of different habitats and niches.

A bright yellow-flowered mutant has appeared on the scene in this setting of pollinator-driven, ecologically opportunistic evolution. In two populations of *M. cardinalis* bright yellow-flowered morphs have become well established. One population is in the Siskiyou Mountains of Oregon, which is the northern limit of the range of *M. cardinalis* (Grant 1924). The other population is on Cedros Island, Baja California, and is at the southern limit of the species range. As Mayr (1976) suggests, new forms often evolve from isolated populations such as these on the periphery of a species

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[1] The opening talk in the symposium, "Mechanisms of Speciation in Higher Plants," given 1 September 1993 at the XV International Botanical Congress, Yokohama, Japan.

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TABLE 1. Nectar production in the species of section *Erythranthe* measured at 0800 h in the wild (Vickery and Sutherland 1994). Averages are based on 20 or more measurements from a population representative of each species or variety.

Species	Volume in μl	% sugar
M. cardinalis	3.9	11.5
M. verbenaceus	6.7	5.8
M. rupestris	0.9	19.0
M. eastwoodiae	1.5	13.7
M. nelsonii	18.3	19.2
M. lewisii		
Rocky Mountains	0.5	0.5
Sierra Nevada	0.7	11.3

range adjacent to new ecological opportunities. A bright yellow-flowered morph of *M. verbenaceus* has appeared also and become well established in a population growing in an isolated spring area, Vasey's Paradise, at the bottom of the Grand Canyon of the Colorado River, AZ, that species' northwestern limit.

Flower colors in section *Erythranthe* are due to various combinations of six anthocyanin pigments—three pelargonidins (apricot-pink) and three cyanidins (lavender-pink)—and at least one carotene pigment (Pollock et al. 1967). The lavender to magenta flowers of *M. lewisii* are due to various combinations of the pelargonidin and cyanidin anthocyanin pigments without the yellow carotene. Flowers of the red-flowered species have all or most of the six anthocyanin pigments plus the carotene pigment. Red color results from a visual blend of pink pigments and yellow pigment. Yellow-flowered plants have a pair of recessive genes at one locus that suppresses anthocyanin production (pink pigments), leaving just the yellow carotene pigment showing. *So, a single mutation, when homozygous, changes flower color from red to yellow.*

If the change from red to yellow flowers leads to a change in pollinators, for example, from hummingbirds to bumblebees or hawkmoths, then the first major step in reproductive isolation has been established by a single gene change (when homozygous)! Once reproductive isolation has been established by color differences, presumably selection would fine-tune it, e.g., by favoring more tubular flowers for hummingbird-pollinated flowers and by favoring a landing platform morphology and nectar guides for bee-pollinated flowers.

Are pollinators required for seed set in *Mimulus cardinalis* or do the flowers self-pollinate? To test these two questions, I used the fact that *M. cardinalis* flowers are borne in pairs. I grew plants of red- and of yellow-flowered *M. cardinalis* from Cedros Island in the greenhouse of the Biology Department, University of Utah. The greenhouse is free of pollinators. I carefully hand-pollinated one flower of each of ten pairs of red flowers and of ten pairs of yellow flowers. The hand-pollinated flowers of both the red-flowered and yellow-flowered plants set moderate numbers of seeds per capsule (50–150), while the unpollinated flowers set no seeds at all. This finding corroborates my earlier observations on the Cedros Island *M. cardinalis* (Vickery 1990) that flowers do not self-pollinate and that pollinators are required for seed set.

Are the rewards for pollinators the same in yellow flowers as in red? That is, do yellow flowers and red flowers produce equal volumes of nectar with the same concentrations of sugars? Red flowers of the Cedros Island *M. cardinalis* produced an average (based on flowers from 30 greenhouse-grown plants) volume of 9.5 μl of nectar with 18.2% sugar. Yellow flowers produced an average (based on measurements of flowers from 40 greenhouse-grown plants) of 10.9 μl of nectar with 23.0% sugar. There is so much variation that these values are not significantly different.

Finally, the key question, do pollinators show a preference for red or yellow flowers? To study this question, I placed 24 red-flowered and 24 yellow-flowered plants in a random arrangement in a meadow in the Red Butte Canyon Natural Area in the Wasatch Mountains behind the University of Utah and observed pollinators that visited this experimental population. Pollinators that came were hummingbirds and bumblebees, with rare visits from flies, but no hawkmoths or honey bees. Pollinators were observed for three 50-min periods on each of 5 d. On 28 July 1987 there were 55 hummingbird visits to the 39 red flowers present and 20 visits to the 35 yellow flowers. Chi-square = 14.379, $p < .001$, which indicates a significant preference for red flowers. That day there were 10 bumblebee visits to red flowers and 12 to yellow flowers. Chi-square = 0.1818, no significant preference. On 31 July there were 176 hummingbird visits to the 42 red flowers in bloom that day in the population and 40 visits to the 21 yellow flowers. Chi-square = 70.246, $p < .001$, which indicates a significant preference for red. That day there were six bumblebee visits to red and one to yellow. There were too few bumblebee visits for a meaningful x^2 value to be calculated. The same pattern of three observation periods was continued on 2–4 August, but once again there were too few pollinator visits to obtain meaningful x^2 values. Apparently, most hummingbirds had migrated south and there were few bumblebees all season that year. On the first day of the experiment when the plants had just been placed in the meadow all pollinators would be naive for both red- and yellow-flowered *M. cardinalis* plants inasmuch as Red Butte Canyon is hundreds of miles from the nearest *M. cardinalis* population in northern Arizona. Therefore, the highly significant preference for red appears to be real and not the result of learned behavior. Apparently, hummingbirds strongly preferred the red flowers but also visited the yellow flowers to some extent. The few bumblebee visits did not suggest a preference.

Results show that the change in flower color from red to yellow did affect the frequencies of pollinator visits, but not in an all-or-none way that would immediately establish reproductive isolation. However, the change would probably be enough to initiate partial, incipient reproductive isolation.

Would *M. verbenaceus* with its normal red morph and mutant yellow morph produce the same reactions in pollinators? The flowers of *M. verbenaceus* differ from those of *M. cardinalis* in that only the upper two corolla lobes are reflexed, whereas all five of those of *M. cardinalis* are reflexed. Both species sometimes have wild populations with orange-red flowers instead of the typical red flowers.

For the *M. verbenaceus* experiment, plants of red-flowered and yellow-flowered individuals from Vasey's Paradise in the Grand Canyon plus plants of an orange-red–flowered population from Yecora, Sonora, Mexico, were placed on a lawn by clumps of native Gambel oak at the mouth of Parley's Canyon, Salt Lake City, UT. This location had an abundance of pollinators in contrast to the paucity of pollinators in the Red Butte Canyon meadow used previously. The test population was observed for 15 periods of 1 h each at different times of day from 26 July through 8 August 1988. On average, there were 73 red flowers, 87 orange flowers, and 136 yellow flowers (see Vickery 1990 for daily details of numbers and chi-square calculations). On average, bumblebees visited them 24, 56, and 128 times, respectively; and hummingbirds 43, 98, and 52 times, respectively (Vickery 1990). Bumblebees significantly eschewed red and orange flowers and preferentially visited yellow flowers. Hummingbirds significantly preferred orange, visited red flowers in proportion to their frequency in the population, and significantly eschewed yellow flowers. Results for *M. verbenaceus* are much clearer than those for *M. cardinalis*. There is a definite preference for yellow by bumblebees and a clear avoidance of yellow by hummingbirds. Thus, this color change has lead to significant, partial isolation between the normal orange- and red-flowered morphs and the yellow-flowered mutant morph under the conditions of this experiment.

Would *M. cardinalis* react like *M. verbenaceus* in the better experimental locality at the mouth of Parley's Canyon? To probe this question, I added red-, orange-, and yellow-flowered morphs of *M. cardinalis* to the *M. verbenaceus* red-, orange-, and yellow-flowered morphs of the previous experiment. The new experiment was run 8–17 August 1988, with the population being observed for 15 periods of 1 h each at different times of day. On average there were 61 red, 57 orange, and 22 yellow flowers of M. cardinalis (see Vickery 1990 for day-to-day numbers and chi-square calculations). On average, bumblebees visited them 28, 30, and 29 times, respectively, and hummingbirds 59, 60, and 6 times, respectively. Bumblebees eschewed red and orange flowers and significantly preferred yellow flowers despite their low numbers in the population. Hummingbirds significantly eschewed yellow flowers and preferentially visited orange flowers. *M. verbenaceus* plants were run again at this time with *M. cardinalis* plants and exhibited the same attractiveness or lack of attractiveness to the pollinators as before. The presence of *M. cardinalis* flowers did not alter pollinator response to *M. verbenaceus* flowers. The color shift from red (or orange) to yellow leads to marked, partial reproductive isolation in *M. verbenaceus* as well as in *M. cardinalis*.

How effective is the partial reproductive isolation? To test this, I placed 198 plants of *M. verbenaceus*—one-sixth yellow-flowered and five-sixths red-flowered to simulate a population with a well-established mutant—in four experimental areas: the experimental garden on the University of Utah campus, Red Butte Canyon Natural Area, the mouth of Parley's Canyon, and at Silver Fork, Big Cottonwood Canyon, Salt Lake County, UT. I harvested seeds of each plant and planted seeds harvested from 20 yellow-flowered plants and grew them to flowering. If pollinators were visiting the flowers at random, then they should pick up and carry pollen from red flowers five times more often than pollen from yellow flowers. Pollen loads and resulting seed sets were well below the 500–1500 seeds per capsule that may occur in *M. verbenaceus*. So, results were not skewed by saturation of the stigma. Also, assuming all else to be neutral such as relative growth rates of yellow- and red-pollen tubes, speed of flowering of red- and yellow-flowered plants, randomness of placement of red- and yellow-flowered plants, and sample size of red- and yellow-flowered plants, then the expected five-to-one visitation rate should hold. Inasmuch as red is genetically dominant to yellow, then five-sixths of the seedlings should be red-flowered and one-sixth yellow-flowered; that is, of the 214 seedlings grown, 178 should be red-flowered and 36 yellow-flowered. In fact, there were 86 red-flowered seedlings and 128 yellow-flowered seedlings. The ratio is 2 red to 3 yellow flowers, which is far from the expected ratio of 5 red flowers to 1 yellow flower. This suggests considerable pollinator faithfulness to one color or the other. However, in addition to pollinator faithfulness there could be self-pollination. *Mimulus cardinalis* does not self-pollinate but *M. verbenaceus* does at the average rate of 10 seeds per capsule. Average normal seed set is 110 seeds per capsule. Therefore self-pollination would account for 9% of the yellow-flowered seedlings; i.e., 9% of the 214 seedlings, or 19 seedlings, would be expected to be yellow-flowered as a result of self-pollination. Of the remaining 195 seedlings, five-sixths, or 162, would be expected to be red, and one-sixth, or 33, would be expected to be yellow. Therefore, I should expect to observe 162 red-flowered seedlings and 52, i.e., 33 + 19 (the results of self-pollination), yellow-flowered seedlings instead of the 86 red-flowered and 128 yellow-flowered seedlings actually observed. This is a highly significant difference ($x^2 = 146.730$, $p < .0001$) and greatly strengthens the point of pollinator faithfulness. Clearly, pollinator preference for yellow and faithfulness to yellow are having a large effect, though not an all-or-none effect. We are seeing strong incipient reproductive isolation due to color change. In different areas with different conditions and different guilds of pollinators the effect might be less or might be stronger, even leading eventually to effective reproductive isolation and speciation.

Acknowledgments

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FALL LAMB PRODUCTION BY A CALIFORNIA BIGHORN SHEEP

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Key words: parturition, California bighorn sheep, Ovis canadensis, *Idaho.*

Parturition is timed to maximize survival of offspring (Thompson and Turner 1982). Parturition occurring outside an optimum time period lowers reproductive fitness and, therefore, should be selected against. Timing of parturition in bighorn sheep (*Ovis canadensis*) has been related to resource abundance (Geist 1974, Bunnell 1982, Thompson and Turner 1982, Risenhoover and Bailey 1988) and climatic conditions (Stewart 1982). Parturition varies by latitude between subspecies (Thompson and Turner 1982) and by elevation within subspecies (Risenhoover and Bailey 1988). Peak lambing periods occur in March for desert bighorn sheep (*O. c. nelsoni;* Hanson 1960, Sandoval 1980, Witham 1983), May for California bighorn sheep (*O. c. californiana;* Jones 1950), and early June for Rocky Mountain bighorn sheep (*O. c. canadensis;* Bunnell 1982, Thompson and Turner 1982). Unusual lambing periods such as January for desert bighorn (Russo 1956, Welles and Welles 1961) and July for Rocky Mountain bighorn (Stewart 1982) were attributed to extremes in climatic conditions and elevations.

Vegetation in the Big Jacks Creek drainage, Owyhee County, ID, is dominated by sagebrush (*Artemisia* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), and Sandberg bluegrass (*Poa sandbergii*). Climatic conditions are characterized by warm, dry summers and cool winters. Total precipitation from November 1988 through March 1989 was equal to the 10-year average; however, most precipitation occurred as rain in November and March. Ten ewes, one ewe lamb, and three ram lambs from Chilcotin, BC, and two rams from East Fork Owyhee River, ID, were transplanted to Big Jacks Creek during February and March 1988. Four ewes were fitted with radio-collars and periodically located to monitor their movements and status. Three radio-collared ewes were observed with lambs in May 1988. A fourth collared ewe (34) was observed with a lamb (A) less than two weeks old (based on size and behavior) on 26 October 1988. An average gestation period of 174 days for bighorn sheep (Shackleton et al. 1984) indicated conception occurred about 25 April 1988. Ewe 34 and lamb A were located monthly through March 1989. During 1987–1990, onset of parturition occurred from 11 April to 3 May, and mating activity was observed between October and December in an adjacent drainage. The birth of lamb A occurred approximately six months out of cycle. Ewe 34 was observed 4 January 1990 with a lamb (B) that appeared to have been born during the normal lambing period (April–June 1989). Lamb B was conceived between October and December 1988 while ewe 34 was nursing lamb A.

Ewe 34 may not have bred in 1987, or stress related to transplanting may have caused her to abort. Stress can affect any aspect of reproduction (DeForge 1976). Contact with rams during March and April 1988 may have caused ewe 34 to come into estrus. Presence of males has been found to induce estrus in female merino sheep (Watson and Radford 1960) and feral goats (Coblentz 1980). Recurrent estrus was observed in a cow elk (*Cervus elaphus*) that was associated with bulls but not bred during previous estrus periods (Morrison 1960).

Lamb survival has been related to forage quality (Wehausen et al. 1987, Festa-Bianchet

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1988a), precipitation patterns (as they affect plant growth; Douglas and Leslie 1986), population density (Douglas and Leslie 1986), and mother's age (Festa-Bianchet 1988a). Cheatgrass brome (*Bromus tectorum*) seedlings were available in November, and Sandberg bluegrass greenup was observed in January. South-facing slopes were generally free of snow soon after storms. Cattle grazing occurred in riparian areas and on plateaus adjacent to drainages, areas that received limited use by bighorns during summer and lambing periods. Bighorn and mule deer (*Odocoileus hemionus*) populations were at low densities. Competition for forage was probably not a limiting factor. Festa-Bianchet (1988b) reported that lambs born to ewes four to nine years old had significantly higher survival rates than those born to two- to three-year-old ewes. Ewe 34 was estimated to be five years old in 1988. Mild climatic conditions, availability of green forage during weaning, limited competition for forage, and probable previous lambing experience allowed ewe 34 to raise an out-of-season lamb and survive concurrent fall/winter lactation and gestation periods. This observation suggests that under favorable conditions bighorn sheep may be able to successfully reproduce outside generally observed reproductive periods.

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AGE, GROWTH, AND REPRODUCTION OF LEATHERSIDE CHUB (*GILA COPEI*)

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Key words: Gila copei, *leatherside chub, life history, reproduction, age, growth.*

The leatherside chub (*Gila copei*) is a small cyprinid native to eastern and southern areas of the Bonneville Basin of Utah, Idaho, and Wyoming, to Wood River, Idaho, and to regions of the Snake River, Idaho and Wyoming, above Shoshone Falls (Baxter and Simon 1970, Simpson and Wallace 1982, Sigler and Sigler 1987). *Gila copei* is currently listed as a candidate for federal protection under the Endangered Species Act.

Conservation efforts for *G. copei* would benefit from accurate life history data, yet the life history of *G. copei* is not well known. This species was thought to live less than five years (Sigler and Sigler 1987). Based on bright coloration of males and abdominal distension in females, Sigler and Miller (1963) concluded *G. copei* spawns between June and August. Using similar coloration criteria on males from Sulphur Creek, WY, Baxter and Simon (1970) suggested breeding occurred in late summer; Simon (1951) found females distended with eggs in early August. Other than these few observations, no data on age, growth, or reproduction are available.

We present data on age, growth, and reproduction of leatherside chub from central Utah; these data were generated as a first step to understanding and protecting this potentially threatened, endemic fish species.

STUDY SITE

Age and growth data were obtained from 36 *G. copei* collected from Thistle and Main creeks, both tributaries to larger rivers that flow into Utah Lake. Thistle Creek, a tributary to Spanish Fork River, was sampled in May, September, and October 1993 ($n = 25$) (39°52′N, 111°32′W) at an elevation of approximately 1700 m. Main Creek flows directly into Deer Creek Reservoir (an impoundment of Provo River) and was sampled in July 1993 ($n = 11$) 500 m upstream from the reservoir (40°24′N, 111°28′W) at an elevation of 1650 m. Chubs used for determining reproductive patterns (below) were collected from the latter site in 1978–79. Creeks at both locations flow slowly at low gradient through meadows. The Main Creek site is downstream from beaver dams; tall grasses and small trees grow along banks. Collections for both creeks were made from vegetated pools separated by shallow riffles; stream substrate is silt, gravel, and boulders.

MATERIALS AND METHODS

Because *Gila copei* is a species of special concern, our permit was limited to 40 specimens, and care was taken to collect the entire size range. Following collection by electroshocking, fish were placed on ice and transported to Brigham Young University (BYU) where they were stored frozen. Individuals were then thawed, rinsed in water, blotted dry, and weighed (0.001 g) on a Denver Instrument XD-1200D® electronic balance; standard length (SL) was determined (0.01 mm) using Fowler Ultra Cal III® electronic calipers.

Ages were determined by grinding otoliths (lapilus) to a thin section and counting opaque bands under a Leica dissecting microscope (40X). Opaque bands were validated as annuli using a marginal increment analysis; because juvenile (ages 1–2) and adult fish (ages 3–8) demonstrated distinct growth rates, they were evaluated separately. Identification of annuli was facilitated by generating digitized images of otoliths on a video monitor using a Hitachi

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CCTV® camera fitted to a Heerbrugg Wild® dissecting microscope. Annual growth increments along the longest axis of the otolith were then measured (0.001 mm) using video image analysis software (Mocha release 1.0, Jandel Scientific; Rundel 1993), which reduces measurement errors introduced when reading otoliths directly under a microscope (McGowan et al. 1987).

Size at age was back-calculated from otolith measurements using a modified Fraser-Lee formula (Campana 1990):

$$L_x = L_0 + (L_c - L_0)(R_x - R_0)/(R_c - R_0),$$

where L_x is estimated SL at age x, L_c is length at capture, R_x is otolith radius at age x, and R_c is otolith radius at capture. L_0 is estimated length at swim-up (estimated at 4 mm from data on *Gila atraria*; Varley and Livesay 1976), and R_0 is otolith radius at swim-up (estimated from otoliths at 0.01 mm).

There was no significant difference in back-calculated lengths at age I between Main and Thistle creek chubs (Main Creek, $n = 11$; Thistle Creek, $n = 25$; T = 1.96, d.f. = 34, $P = .06$) . Numbers of age II ($n = 2$) and age III ($n = 3$) fish from Main Creek precluded statistical comparisons; however, back-calculated lengths at age II and age III for Main Creek fish were within the range of comparably aged fish from Thistle Creek. Hence, growth data for the two populations were combined. An age-growth curve was generated for the combined samples by averaging back-calculated sizes at age.

Leatherside chub collected in 1993 were sexed by dissection and examination of gonads; individuals lacking mature gonads were classified as juveniles. Immature testes were translucent and threadlike, while mature testes were opaque (white or pinkish) and firm. Reproductive states of ovaries were determined according to criteria in Holden and Berry (1983); immature ovaries were small, translucent, and lacked yolked ova; mature ovaries were larger and contained both immature ova and firm, yolked ova.

Reproductive data were obtained from a collection of 176 adult leatherside chubs archived in the Monte L. Bean Museum at BYU (#5592–5619, 5629–5686, 5688–5775). Monthly collections from Main Creek (August 1978 to September 1979) were made using minnow traps, hand nets, and electrofishing gear, and preserved in formalin. Daily temperature was recorded from September 1978 to July 1979.

Standard length was measured (mm), and preserved wet mass (0.01 g) was recorded, for each specimen. Gonads from all ($n = 176$) individuals >50 mm SL were removed and weighed (0.001 g). No fish <50 mm SL had enlarged gonads. A gonadosomatic index (GSI) was generated for each fish using the following formula (Andreasen and Barnes 1975):

$$\text{GSI} = (\text{gonad weight} / \text{body weight}) \times 100.$$

Mean monthly GSI values were used to determine onset and duration of spawning. Ova counts were made on nine fish collected in May 1979. The relationship between number of ova present and SL was evaluated by linear regression.

RESULTS

Opaque bands on leatherside chub otoliths appear to be valid annuli as demonstrated by an increase in the marginal growth increment throughout the growing season for both adult and juvenile fish (Fig. 1).

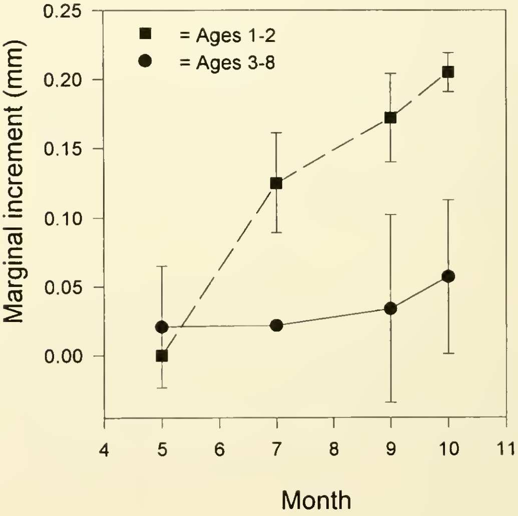

Fig. 1. Mean marginal increment widths (±2 S.E.) measured from otoliths in *Gila copei* ($n = 36$). Immature age classes (1–2) and mature age classes (3–8) plotted separately.

Ages of 36 *G. copei* collected in 1993 ranged from one to eight years, with SL of 38–110 mm (Table 1). Chubs grew rapidly to ~58 mm SL at about age II (Fig. 2, Table 1). From age II on, annual growth was slower and fairly uniform. Mean GSI values for males and females (Fig. 3a) were highest for both sexes in spring with maxima in May (female GSI = 12.3, male GSI = 2.7). Increasing water temperatures from January through May (Fig. 3b) were associated with increased GSI values for both sexes. Average water temperature in May, corresponding to GSI maxima, was 9.4° C.

Fecundity (as measured by ovum counts) increased with SL for females collected in May 1979 and ranged from 938 in a 67-mm-SL, 5.9-g female to 2573 in a 92-mm-SL, 14.6-g female. Average count for leatherside chubs collected in May 1979 was 1813. Significant correlations existed between SL and fecundity ($R^2 = .82$, $P < .05$, $n = 9$) and weight and fecundity ($R^2 = .72$, $P < 0.05$, $n = 9$).

DISCUSSION

A maximal age of eight years in our sample of *G. copei* indicates a life span much longer than previously thought (Sigler and Sigler 1987). Longevity in *G. copei* may be a life history trait that has evolved in response to living

TABLE 1. Capture and back-calculated standard lengths (SL) of *Gila copei* from Thistle and Main creeks, central Utah.

		SL at capture		Mean back-calculated SL at annulus							
Age	*N*	Mean	Range	1	2	3	4	5	6	7	8
1	8	44	38–49	32							
2	9	76	65–85	41	65						
3	2	87	71–104	42	68	82					
4	1	85	—	51	65	77	83				
5	1	97	—	38	53	70	87	96			
6	7	92	83–110	35	52	63	73	82	89		
7	7	94	88–105	36	54	66	73	80	86	91	
8	1	96	—	31	46	54	62	67	76	86	93
Overall means				37	58	67	74	81	87	90	93

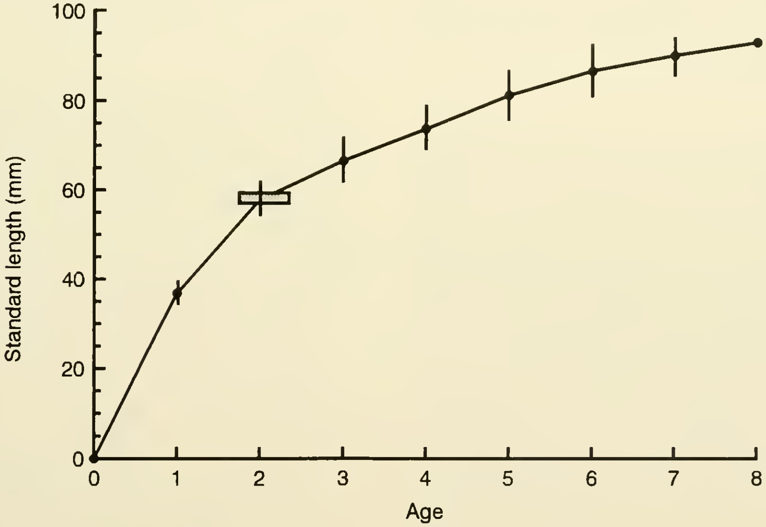

Fig. 2. Mean back-calculated standard lengths at age (±2 S.E.) for *Gila copei* ($n = 36$) in central Utah. Shaded block indicates estimated age at first reproduction.

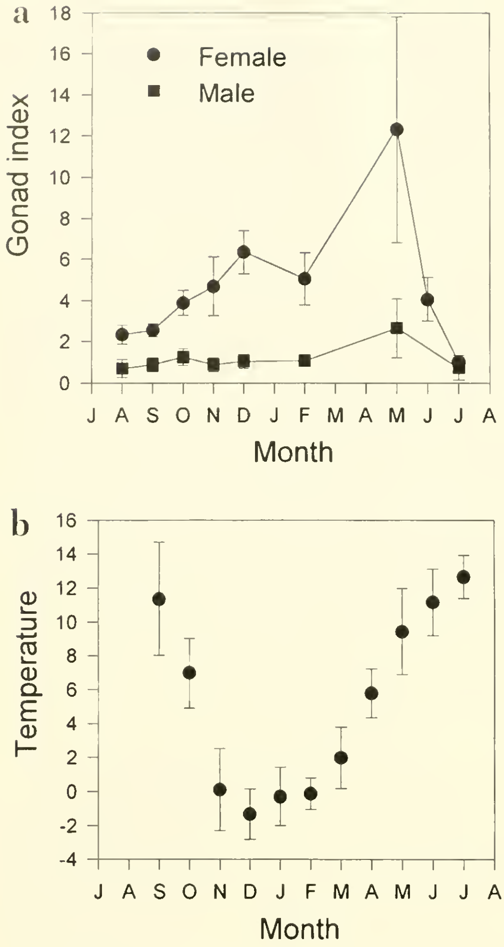

Fig. 3a. Mean gonadosomatic indices (±2 S.E.) for male and female *Gila copei* (n = 176); b, mean monthly temperatures (±2 S.E.) from August 1978 to July 1979 in Main Creek, Wasatch County, UT.

in an environment where annual precipitation and stream flow vary considerably. Successful chub reproduction and recruitment may be uncertain in any given year. An extended life span would increase the likelihood that appropriate environmental conditions for reproductive success would be met at some time in an individual's life; thus, longevity may be a "bet-hedging" strategy (Stearns 1976) for living in unpredictable conditions.

The growth pattern of *G. copei* is typical of other fishes in which rapid juvenile growth decreases at the onset of sexual maturity as finite energy resources are allocated to both growth and reproduction (Roff 1984). The inflection point in the growth curve (Fig. 1), coupled with the facts that the smallest fish with developed gonads collected in 1993 was 65.2 mm SL and no fish in the museum collection <50 mm SL had enlarged gonads, suggests that first reproduction in *G. copei* occurs at age II.

High GSI in May followed by decreased GSI in June and minimal values in July and August (Fig. 3a) indicates that peak spawning occurred in May, with some activity possibly extending into early June. *Gila copei* apparently follows a pattern of reproduction common to various cyprinids living in temperate climates (Munro et al. 1990). This pattern is characterized by the onset of spawning in late spring followed by a period of gonadal recrudescence and inactivity; size of gonads begins to increase in autumn and continues through winter, with final maturation occurring in early spring.

If temperature influences the onset of spawning, differences in temperature (as a function of latitude) between Main Creek (this study) and southwestern Wyoming (Simon 1951) could explain the discrepancy between onset of chub spawning at these locations (May vs. August). A more detailed investigation of *G. copei* will be required to resolve questions of differences in reproductive and life history characteristics among populations.

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CONSUMPTION OF A TOXIC PLANT (*ZIGADENUS PANICULATUS*) BY MULE DEER

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Key words: death camas, Zigadenus, *mule deer, poisonous plants, coevolution.*

The abundance of green vegetation in nature can yield false impressions of the availability of food resources to herbivores because many plants have evolved anti-herbivore defenses. Defensive mechanisms commonly include incorporation of distasteful or toxic secondary chemical compounds into plant tissues. Effects of different compounds on consumers range from mild (unpalatable) to severe (illness or death from poisoning). Herbivores have consequently evolved a host of means for coping with defensive compounds, resulting in an evolutionary arms race between plants and herbivores (Freeland and Janzen 1974). Although evidence of plant/herbivore coevolution can be found for herbivores ranging from phytophagous insects to mega-vertebrates, we concentrate specifically on mule deer (*Odocoileus hemonius*) feeding on toxic plants.

Because domestic grazing animals lack a coevolutionary history with the plant communities in which they forage, they are often affected by toxic secondary compounds to a greater degree than native herbivores. This has significant economic impact on the range livestock industry due to direct losses, such as death, reduced fecundity, or reduced weight gain, and to indirect costs of minimizing such losses (Nielsen et al. 1988, James et al. 1992). Historical familiarity with local plant assemblages has provided herbivores foraging in their native ranges with two advantages over introduced domestic counterparts (Freeland and Janzen 1974, Laycock 1978, Laycock et al. 1988). First, native mammals often avoid eating toxic plant species that are eaten by domestic grazers. For example, toxic plants eaten by livestock, such as azalea (*Azalea* spp.) and larkspur (*Delphinium* spp.), are avoided by mule deer even when these plants are abundant (Dixon 1934). Second, in most cases of native ungulates eating a plant species that is toxic to domestic animals, the plant does not produce noticeable toxic effects in the former, indicating that native herbivores may possess detoxification mechanisms for some plant toxins (Laycock 1978). Thus, deer consume without adverse effects a variety of plants poisonous to livestock (Stoddart and Rasmussen 1945, Dean and Winward 1974). Reciprocal examples in which native plants are toxic to native herbivores, but benign to domestic animals, are lacking in the literature.

Herein we report on four years of observations of an eastern Sierra Nevada mule deer herd feeding on substantial quantities of foothill death camas (*Zigadenus paniculatus*), a liliaceous bulb plant that is toxic to domestic sheep, cattle, and horses (Fleming et al. 1921, Kingsbury 1964, James et al. 1980, Panter et al. 1987). The genus *Zigadenus* includes several species, all containing toxic steroidal alkaloids (James et al. 1980). Death camas emerges earlier than most plants, making it particularly hazardous for spring grazing of livestock (Panter and James 1989). These plants have been variously described as "the most important poisonous plants in the western U.S." (Kingsbury 1964) and "the most dangerous poisonous plants in North America" (Clarke and Clarke 1975). Foothill death camas has been described as one of the more toxic *Zigadenus* species (Kingsbury 1964, James et al. 1980).

Our study site is located at T20N, R18E, S36 just west of Reno, NV, on an alluvial fan at the southern base of Peavine Mountain. Woody vegetation is dominated by basin big sagebrush (*Artemisia tridentata tridentata*) and bitterbrush (*Purshia tridentata*). Death camas emerges at this site in mid-March, flowers in

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April, and remains green into May. A herd of mule deer, usually numbering 20–25 animals, has foraged extensively in this area from October to May since we began making observations in fall 1988.

We first noticed deer consuming death camas on 28 March 1989 (before plants flowered) and confirmed this with additional observations in all subsequent years. Examination of death camas foliage immediately after deer left the foraging patches consistently revealed fresh herbivore damage. We found that deer herbivory left a characteristic leaf damage pattern, with most or all leaves of a foraged plant cleanly bitten off perpendicular to their long axes. In addition to direct observations of deer consuming death camas, fresh deer pellet groups were found in patches of plants exhibiting this characteristic damage pattern during all five springs (1989–1993). During observation periods we found no evidence of deer exhibiting toxic effects from death camas consumption, and neither we nor personnel from the Nevada Department of Wildlife (which surveys deer in the area by air) have found any fresh deer carcasses in the vicinity.

Each year from 1990 through 1993 we walked 10–12 permanently located, parallel transects and categorized all death camas plants seen as either eaten or uneaten by deer. Transects were 500 m long, 20 m wide (i.e., we generally saw all plants occurring <10 m from the transect lines), and spaced 30 m apart. Usually, deer removed only the distal 2–5 cm of leaves, but on several occasions we found plants eaten to within 2 cm of ground level. Plants were considered eaten regardless of the amount of leaf removed. We tested these data for temporal differences in frequency of death camas consumption by comparing numbers of eaten versus uneaten plants among the four years of the study using a *G*-test of independence. We similarly tested for spatial effects on consumption by comparing eaten versus uneaten plant counts among individual transect lines within years.

There are at least two potential explanations for the partial consumption of leaves that we noted. Perhaps ends of leaves are less toxic than leaf bases, and deer preferentially consume less-toxic plant parts. Kingsbury (1964) suggests that death camas bulbs are the most toxic part of the plants, and a gradient of decreasing toxicity could occur from bulbs to ends of leaves. Alternately, deer may occasionally sample plants in their environment (Freeland and Janzen 1974), and removal of short leaf segments may represent cautious sampling of a plant deer find undesirable. The latter possibility (sampling) seems less likely than the former (selectivity) because we have observed individual deer feeding on several death camas plants consecutively. Furthermore, total numbers of plants consumed on our transects were several orders of magnitude greater than the number of deer foraging in the study area, and it seems unlikely that deer would have to sample repeatedly so many plants to discover they are undesirable.

We found significant annual variation in the frequency of death camas consumption, ranging from 3.8% to 18.9% of total plants counted showing evidence of deer herbivory ($G = 232.8$, $df = 3$, $P < .0001$; Table 1). Maximum and minimum percentages of plants eaten (Table 1) illustrate that frequency of herbivory also varied spatially; in each of the four years we sampled there was significant variation among transects in numbers of plants eaten ($P < .001$ for all years). While the minority of plants in the local death camas population were eaten, the values in Table 1 also represent a surprisingly high frequency of herbivory on a plant species with such a notorious reputation.

The relatively low proportions of damaged plants indicate that deer may be selective for particular death camas plants. This is supported by the fact that deer generally ate only a few non-neighboring plants from large patches of death camas; rarely did the majority of plants within a patch show evidence of herbivory. The apparently selective use of individual death camas plants, significant temporal and spatial variation in death camas use, and infrequent extensive herbivory on small patches of plants could be due to variation among plants or patches in toxicity or to differing availabilities of superior foods leading to variation in the use of toxic foods.

Our observations suggest that death camas is more palatable to deer than to domestic cattle or sheep. Domestic animals must be force-fed death camas in captivity experiments (Fleming 1918, Fleming et al. 1921, Panter et al. 1987) and must be stressed or left with few alternative foods in nature before they consume it (Panter et al. 1987). Mule deer at our study site, however, occur at a low density and consume

TABLE 1. Numbers and percentages of foothill death camas plants consumed by mule deer along 500-m transects, 1990–1993, at Peavine Mountain (Washoe County, NV).

Year	Number of transects	Number of plants[a]		Plants eaten per transect (%)		
		Total	Eaten	Maximum	Minimum	$\bar{X}$ ± S.D.
1990	12	2646	501	29.0	7.3	18.6 ± 10.6
1991	12	2726	259	44.7	2.6	16.4 ± 13.4
1992	10	3073	118	32.6	1.6	8.3 ± 9.6
1993	10	3799	202	15.4	2.5	8.0 ± 4.0

[a] Includes combined data from all transects.

death camas each spring although alternative plants are available. Because bitterness is a general property of alkaloids (Laycock 1978), death camas is quite bitter. Most herbivores apparently find bitterness distasteful (Laycock 1978); however, bitterbrush (*Purshia tridentata*), which is named for its bitterness, is a preferred browse plant of mule deer. Although bitterbrush is also consumed by domestic ungulates, it is not highly preferred by them, perhaps because bitterness is a greater feeding deterrent to domestic animals than to deer.

Native herbivores have been observed consuming a variety of plant species known to be toxic to domestic herbivores (Laycock 1978), including an anecdotal report of mule deer in Utah consuming death camas and several other toxic plants (Stoddart and Rasmussen 1945). Recent work stimulates the interesting possibility that herbivores consume specific toxic plants to rid themselves of gut parasites (Barbosa et al. 1991, Gauld and Gaston 1992). However, this hypothesis only addresses why toxic plants are consumed rather than why the consumers are physiologically able to tolerate the toxins. Although we can only speculate about reasons mule deer are less affected by death camas toxicity than domestic ruminants, a likely explanation is that deer possess rumen microflora that have acquired the ability through natural selection to detoxify this plant (Freeland and Janzen 1974, Laycock 1978). Such selection is perhaps to be expected for native ruminants because the microflora community has seen prolonged exposure to native toxic plants. It is certainly possible, however, that deer are able to detoxify death camas by some other mechanism. For example, since deer are browsers, their diets include large amounts of tannins (Cooper and Owen-Smith 1985, Robbins et al. 1987) that may precipitate the alkaloids in death camas into a harmless tannate (Freeland and Janzen 1974).

Because even limited past exposure of a herbivore to a particular toxin can result in reduced toxic effects, selection for detoxifying rumen microflora may also account for intraspecific variation in toxicity among individuals of a domestic species. Such individual variation in susceptibility to death camas toxicity has been reported in force-feeding experiments with domestic sheep (Fleming et al. 1921, Kingsbury 1964). Perhaps it is possible to utilize this individual variation in selectively breeding for reduced vulnerability to particular toxins. Currently, most domestic grazing animals are products of artificial selection for productivity, rather than for resistance to environmental challenges.

Another avenue for applied research concerns the possibility of ameliorating effects of toxic plants through the transfer of rumen innocula from animals resistant to specific toxins to those that are susceptible. Jones (1985) reported that transfer of rumen cultures from goats that were resistant to poisoning by *Leucaena leucocephala* to susceptible goats and steers eliminated adverse effects of *Leucaena* consumption in the previously susceptible animals. This example suggests that even interspecific transfer of rumen fluids may effectively reduce toxic effects in some cases.

Deer herbivory we witnessed on Peavine Mountain may affect the demography of the local death camas population. Defoliation experiments indicate that death camas probably suffers reduced reproductive output after herbivory (Tepedino 1982, Knapp 1986). While plants adapted to herbivory may compensate for loss of biomass by allocating additional energy to growth and/or reproduction, highly toxic species instead employ an evolutionary strategy of defense against herbivory and thus may not exhibit compensation (Cates 1975, Laycock 1978). When such defenses are circumvented by herbivores with detoxification mechanisms, toxic plants should experience reduced fitness.

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USE OF AN UNUSUAL FOOD SOURCE BY ROCK WRENS (TROGLODYTIDAE)

Polly K. Phillips[1] and Allen F. Sanborn[2]

Key words: Rock Wrens, food source, foraging, Salpinctes obsoletus, *Troglodytidae, feeding behavior.*

On 12 July 1993 we observed an interesting exchange between an adult Rock Wren (*Salpinctes obsoletus*) and two juveniles. While at Toroweap Point on the north rim of the Grand Canyon we observed an adult wren accompanied by two juveniles near our vehicle. All three birds walked beneath the vehicle by the rear wheel, but the adult moved immediately to the front end whereupon it hopped onto the front bumper and began to inspect the grill. The adult found and ate an insect that had been trapped in the grillwork. While standing on the bumper, the adult began to vocalize after consuming the insect. The juveniles appeared to show a positive phonotactic response to these calls, stopped foraging under the rear of the vehicle, and moved to the front. After the juveniles arrived at the front of the vehicle, the adult continued collecting insects from the grill. The adult ate none of these insects but merely held them in its beak while walking back and forth across the bumper. The adult continued to vocalize, periodically pausing to face the juveniles. Then it continued foraging in the grill. It appeared to us that the adult was showing the insects to the young. Neither of the young birds joined the adult on the bumper, however, and within a few minutes the adult and juveniles flew off, not to return that afternoon. As far as we have been able to determine, this sort of acquired or derived behavior has not been reported previously for Rock Wrens nor for any member of the family Troglodytidae.

Other observers have noticed birds taking advantage of unusual food sources, such as the opening of milk bottles (Fisher and Hinde 1949). There is generally a question, however, as to whether the behavior was by chance or learned. One possible explanation for our observations is that the parent was tutoring the offspring about the availability of food in vehicle grillwork. Tutoring and observational learning have been documented in laboratory experiments in blackbirds (Mason et al. 1984), tits (Sherry and Galef 1984, 1990), and pigeons (Palameta and Lefebvre 1985), and have also been documented in the wild in other birds using usual food sources (Schaadt and Rymon 1982). We have no way of knowing whether the adult we observed was attempting to teach what we believe were its offspring about an unusual food source. We hope this observation will stimulate further study of feeding in fledgling birds with the possibility of discoveries in social learning.

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GREAT BASIN NATURALIST Vol. 55, No. 2, April 1995

CONTENTS

Articles

Diets of young Colorado squawfish and other small fish in backwaters of the Green River, Colorado and Utah .... Robert T. Muth and Darrel E. Snyder **95**

Invertebrate fauna of wastewater ponds in southeastern Idaho.. Karen L. Cieminski and Lester D. Flake **105**

Growth and reproduction in an alpine cushion plant: *Astragalus kentrophyta* var. *implexus* .... Wayne R. Owen **117**

Calileuctra, a new genus, and two new species of stoneflies from California (Plecoptera: Leuctridae) .... W. D. Shepard and R. W. Baumann **124**

Carbon isotope discrimination in the C_4 shrub *Atriplex confertifolia* along a salinity gradient .... Darren R. Sandquist and James R. Ehleringer **135**

Demography of *Astragalus scaphoides* and effects of herbivory on population growth .... Peter Lesica **142**

Lahontan sagebrush (*Artemisia arbuscula* ssp. *longicaulis*): a new taxon................................ Alma H. Winward and E. Durant McArthur **151**

Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) on subalpine fir in northern Utah.................................. E. Matthew Hansen **158**

Seasonal nutrient cycling in *Potamogeton pectinatus* of the lower Provo River .... C. Mel Lytle and Bruce N. Smith **164**

Factors influencing fish assemblages of a high-elevation desert stream system in Wyoming .... Bernard Carter and Wayne A. Hubert **169**

Notes

Speciation by aneuploidy and polyploidy in *Mimulus* (Scrophulariaceae)... Robert K. Vickery, Jr. **174**

Speciation in *Mimulus*, or, Can a simple flower color mutant lead to species divergence?.................................. Robert K. Vickery, Jr. **177**

Fall lamb production by a California bighorn sheep.. Matthew McCoy, Walt Bodie, and ElRoy Taylor **181**

Age, growth, and reproduction of leatherside chub (*Gila copei*) .... Jerald B. Johnson, Mark C. Belk, and Dennis K. Shiozawa **183**

Consumption of a toxic plant (*Zigadenus paniculatus*) by mule deer.................................... William S. Longland and Charlie Clements **188**

Use of an unusual food source by Rock Wrens (Troglodytidae) .... Polly K. Phillips and Allen F. Sanborn **192**

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BENTHIC COMMUNITY STRUCTURE IN TWO ADJACENT STREAMS IN YELLOWSTONE NATIONAL PARK FIVE YEARS AFTER THE 1988 WILDFIRES

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ABSTRACT.—Physical characteristics, benthic macroinvertebrates, and periphyton assemblages in two adjacent headwater streams in Yellowstone National Park were evaluated five years after the 1988 wildfires. The catchment of one stream was burned by wildfire (burned stream) while the other catchment was unburned (unburned stream). Physical measures revealed channel alteration in the burned stream relative to the unburned stream. Periphyton biomass was lower in the burned than the unburned stream (29.2 vs. 50.5 g/m^2 AFDM, respectively), further demonstrating the unstable physical conditions of that system. Kendall's coefficient of concordance (an index of similarity) between diatom assemblages was 0.22, indicating distinct assemblage composition between streams. *Navicula permitis* Hust. was the most abundant diatom in the burned stream while *Hannaea arcus* (Ehr.) Patr. was dominant in the unburned stream. Macroinvertebrate taxa richness, density, and biomass were all greater in the unburned stream, although Chironomidae was the most abundant taxon in both streams. Results suggest the removal of terrestrial/riparian vegetation by wildfire can directly influence stream benthic assemblages by altering the inherent disturbance regime of the physical habitat templet.

Key words: wildfire, streams, disturbance, macroinvertebrates, diatoms, benthic habitat, Yellowstone National Park.

Physical disturbance, acting at various spatial and temporal scales, often is the predominant factor structuring stream benthic communities (Minshall 1988, Resh et al. 1988). Further, physical disturbances may be viewed in a hierarchical framework, with the effects of small-scale disturbances altered (intensified or mediated) by large-scale disturbance events (sensu O'Neill et al. 1986). Wildfire, as a large-scale disturbance, directly influences stream biotic structure and function by affecting the physical habitat of stream ecosystems (Minshall et al. 1989, Minshall and Brock 1991, Richards and Minshall 1992, Robinson et al. 1994, Mihuc et al. in press, Robinson and Minshall in press). In lotic ecosystems, physical disturbance also may constrain the establishment of biotic controls, such as competition and predation, on benthic community structure (McAuliffe 1984, Minshall and Petersen 1985, Resh et al. 1988).

Wildfire burned extensive portions of the Greater Yellowstone Ecosystem during the summer of 1988. Over 32% of the streams in Yellowstone National Park (YNP) were affected to varying degrees by wildfires (Minshall et al. 1989, Minshall and Brock 1991, Robinson et al.

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1994). Minshall and Brock (1991) summarized the immediate effects of the fires on YNP's stream ecosystems and hypothesized on the mid-term (10–25 yr) and long-term (50–300 yr) effects. They suggested that most adverse short-term effects on streams resulted from increased sediment load and channel erosion caused by increased overland runoff following precipitation events and snowmelt. The intensity and frequency of short-term effects were hypothesized to decrease by year 5 as riparian conditions improve (see Richards and Minshall 1992). In general, mid- and long-term effects on streams, including recovery to prefire conditions, should correspond to vegetative regrowth in burned catchments (Minshall et al. 1989, Minshall and Brock 1991).

The present study compared physical characteristics and benthic community structure in two streams five years after the 1988 wildfires. The streams are adjacent second-order (after Strahler 1952) tributaries of the South Fork Cache Creek. The catchment of one stream was burned during the 1988 wildfires, while the catchment of the other was essentially unburned. The spatial arrangement of these streams (adjacent basins) provided a treatment/reference situation where confounding factors of climate and geology are minimized when comparing differences among the study streams. However, the study lacks true replication of the burned and unburned treatments (sensu Hurlbert 1984) and must be viewed as a simple comparison study. Phenomenological studies and/or two stream comparisons are common in stream ecology (e.g., Wallace et al. 1986, Robinson et al. 1993, Scarsbrook and Townsend 1993) and are capable of providing valuable insights (Townsend 1989). The present study can be viewed as a natural "experiment" with observed differences between the two streams attributed to the effects of wildfire. In that context, the study provides insights on general patterns of lotic ecosystem recovery to an unpredictable, large-scale disturbance (Townsend 1989, Lamberti et al. 1991).

METHODS

The study streams, located in the northeast corner of YNP, were surveyed on 19 July 1993. One stream had over 80% of its catchment burned during the 1988 Yellowstone wildfire (hereafter, burned stream; 110°01′30″W, 44°50′00″N), while less than 10% of the catchment of the other stream was burned (hereafter, unburned stream; 110°01′00″W, 44°49′30″N). Climate of the area is typical of the northern Rocky Mountains, with precipitation primarily occurring as snow during the winter months. Both streams drain catchments primarily vegetated (prior to the fire in the burned stream) by coniferous forests of lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmannii*). Riparian vegetation consisted of willow (*Salix*), rose (*Rosa*), and alder (*Alnus*).

Surveys were conducted approximately 0.5 km above the confluence of the two streams. Physical characteristics were measured in each stream at five cross-sectional transects, each situated approximately 50 m apart. Measurements made at each transect included stream width at baseflow, stream width at bankfull discharge, and stream cross-sectional profile (for calculation of width:depth ratios). Discharge was calculated in each stream at the most suitable transect following the methods of Platts et al. (1983). In addition to measurements at each transect, 100 randomly selected rock substrata along a 100-m length of stream (located within the outermost cross-sectional transects) were measured for size (length of the longest axis) and percent embeddedness. Embeddedness was defined as the percent coverage of the rock (three-dimensional surface) by fine sediments. Large boulders that protruded through the water surface were not used in substratum size measurements. Water depth and near-bed water velocity also were recorded at each of the 100 random locations. Near-bed water velocity was measured with a small Ott C-1 current meter approximately 2 cm above each substratum.

One periphyton sample was collected from a suitable (flat-surfaced, medium-sized) rock substratum at each cross-sectional transect using a method described in Robinson and Minshall (1986). Samples were frozen in the field in a Taylor-Wharton 3DS dry shipper charged with liquid nitrogen and returned to the laboratory for processing. In the laboratory, samples were extracted in 10 ml of methanol for 24 h (Holm-Hansen and Riemann 1978). One 3-ml subsample was then removed from each sample and analyzed for chlorophyll *a* using a Gilford Instruments (Model 2600) spectrophotometer. The remaining periphyton material from each sample was used for algal biomass determination, expressed as grams ash-free dry mass (AFDM) per m^2. The material was dried at 50°C for 24 h, weighed on a Sauter balance (Model AR 1014), ashed at 550°C for a minimum of 3 h, rehydrated, redried at 50°C, then cooled to ambient temperature in a desiccator and reweighed. The difference in weights equaled the AFDM of the sample.

Diatom samples were collected in each stream, after Robinson and Rushforth (1987), from three to five rock substrata representing the predominant habitat type (typically riffles). Samples were composited, preserved with 5% formalin, and returned to the laboratory. The composite sample was boiled in concentrated nitric acid, rinsed, mounted in Naphrax mountant, and examined under 1000X oil immersion using a Zeis RA microscope with Nomarski optics (St. Clair and Rushforth 1976). Relative abundances of diatom taxa were determined by counting a minimum of 1000 diatom valves from each stream. Diatoms were analyzed in terms of species richness, Simpson's index, and Kendall's coefficient of concordance (an index of similarity using all taxa with a relative abundance >1%). Other algal groups such as Chlorophyta (green algae) and Cyanobacteria (blue-green algae) were not abundant at the time of sampling and thus were not considered in the present study.

One benthic sample was collected from a riffle/run habitat (pools were rare and not sampled) near each transect and analyzed for macroinvertebrates and benthic organic matter (BOM). Samples were collected using a Surber sampler (250 μm mesh), preserved with 5% formalin, and returned to the laboratory. Woody debris >5 cm in length that was collected in the benthic samples was rinsed of invertebrates and removed from the samples. In the laboratory, macroinvertebrates were hand-sorted from the benthic detritus with the aid of a 3X dissecting microscope, identified to the lowest feasible level (usually genus), enumerated, dried at 50°C for a minimum of 48 h, then cooled to ambient temperature in a desiccator and weighed. Dry weights, in milligrams, were determined on a Cahn (Model 25) electrobalance. The benthic detritus from each sample was used for BOM determination. The quantity of BOM, expressed as g AFDM/m^2, was determined as described above for periphyton. Macroinvertebrates were analyzed in terms of density (no./m^2), biomass (mg/m^2), taxa richness, Simpson's index, and relative abundances.

Chi-squared analysis was used to test for statistical differences in median substratum size between the two streams (Zar 1984). Independent sample *t* tests were used to compare the other characteristics for differences between the two streams. Prior to the *t*-test analysis all data were log $(x + 1)$ transformed, except substratum embeddedness and the relative abundance of invertebrate taxa (both percentage measures), which were arcsine (square root [x]) transformed (Zar 1984). Tabular results are presented as untransformed means and standard deviations. All statistical analyses were performed on SYSTAT (Wilkinson 1990).

RESULTS

Baseflow discharge was equal in the two streams (0.2 m^3/s), reflecting the similar catchment size of the burned (22 km^2) and unburned (26 km^2) streams. Mean baseflow width, near-bed water velocity, and BOM were not significantly different between the two streams ($P > .05$). Substratum embeddedness was significantly greater in the burned stream ($P = .01$), although the difference between mean values was not large (burned = 62.9, unburned = 52.8). It is not known whether this statistical difference was biologically meaningful or simply a reflection of the large sample size ($n = 100$).

Water depth at baseflow ($P < .01$) was lower and stream width at bankfull discharge greater ($P = .03$) in the burned stream than the unburned stream. Although not statistically significant ($P = .06$), the ratio of stream width: depth was greater in the burned than the unburned stream (216 and 91, respectively). The general appearance of the two streams was distinctly different (Fig. 1; Minshall personal observation). Large, woody debris and streamside riparian vegetation, which provide bank and channel stability, were noticeably absent in the burned stream.

Mean substratum size was not significantly different between the two streams ($P > .05$) in 1993, possibly because large boulders were not recorded in the measurements (see Fig. 1). We collected additional data on substratum size in August 1994 and included large boulders in the measurements. Further, substrata within

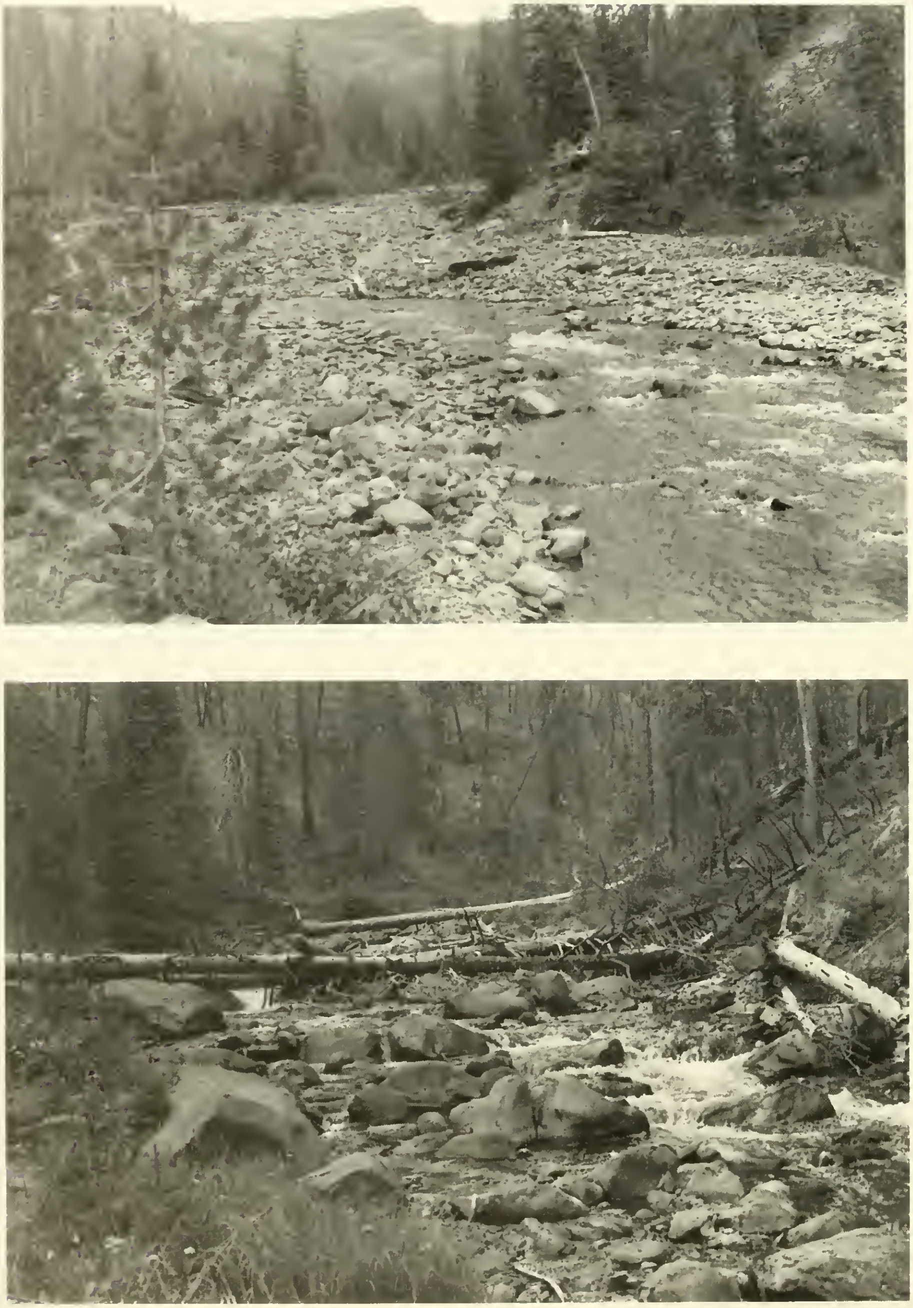

Fig. 1. Representative photographs of the burned (upper) and unburned (lower) streams five years after the 1988 wildfire. Note absence of large, woody debris and streamside riparian vegetation in the burned stream.

the bankfull channel were measured in 1994, in contrast to measures being recorded only within the baseflow channel in 1993. The 1994 results showed that mean substratum size was significantly larger in the unburned than in the burned stream ($P < .01$).

A comparison of median substratum size showed similar results to that of mean substratum size. Median substratum size was not different between the two streams when measurements excluded large boulders and were confined to the baseflow channel ($P > .05$). However, when measurements included large boulders and encompassed the bankfull channel, the difference in median size was significant ($P < .01$). Whether large boulders were present in the burned stream prior to the wildfire has yet to be determined. However, in other streams influenced by intensive wildfire, large boulders were observed to be buried by inorganic debris (primarily gravel and fine sediments) within five years following wildfire (Minshall personal observation).

The burned stream contained less periphyton chlorophyll *a* ($P = .06$) and AFDM ($P < .01$) than did the unburned stream (Table 1). Diatom species richness was greater in the burned (34 taxa) than in the unburned stream (27 taxa; Table 2). Simpson's index was lower for the burned than the unburned stream (0.12 and 0.42, respectively). Kendall's coefficient of concordance for the two diatom communities was 0.22, suggesting distinct assemblage composition among sites. For example, *Navicula permitis* Hust. was the most abundant species in the burned stream, constituting 24.7% of the assemblage, while *Hannaea arcus* (Ehr.) Patr. comprised 63.1% of the assemblage in the unburned stream (Table 2).

Mean macroinvertebrate density and biomass were lower in the burned than unburned stream (Table 3), but the differences were not significant ($P > .05$). For example, mean density in the burned stream was 9960 individuals/m^2, while the unburned stream had 16,950 individuals/m^2, and mean biomass (dry weight) was 1960 and 3200 mg/m^2 in the burned and unburned streams, respectively. Taxa richness and Simpson's index both were reduced in the burned stream, although the difference was significant only for Simpson's index ($P = .04$) (Table 3). The burned stream contained a mean of 15 taxa per benthic sample compared to a mean of 20 taxa for the unburned stream. The mean Simpson's index was 0.57 for the burned stream and 0.73 for the unburned stream. Chironomidae was the most abundant taxon in both streams (Table 4), although their relative abundance was significantly greater (P = .03) in the unburned stream. There were no statistical differences ($P > .05$) in relative abundances of other taxa common to both streams (Hydracarina, Simuliidae, *Baetis bicaudatus*, *Cinygmula*, and *Zapada columbiana*).

DISCUSSION

Alterations of the surrounding terrestrial landscape by major unpredictable disturbances such as hurricanes, volcanic eruptions, or wildfire directly influence streams draining the

TABLE 1. Means (SD) and *P* values for physical characteristics measured in the study streams.

	Burned		Unburned		*P* value
Baseflow width (m)	5.9	(2.6)	4.5	(1.8)	.46
Near-bed velocity (cm/s)	10.3	(0.1)	10.7	(0.1)	.71
BOM (g/m^2)	1.5	(0.8)	2.5	(1.2)	.20
Embeddedness (%)	62.9	(28.5)	52.8	(30.0)	.01
Baseflow depth (cm)	16.9	(11.0)	24.3	(12.5)	<.01
Bankfull width (m)	35.0	(11.9)	16.6	(1.4)	.03
Bankfull width:depth ratio	216	(101)	91	(21)	.06
Periphyton chl *a* (mg/m^2)	8.9	(5.5)	32.1	(19.5)	.06
Periphyton AFDM (g/m^2)	29.2	(3.7)	50.5	(9.3)	<.01
*Mean substratum size (cm)	14.4	(10.5)	15.0	(14.2)	.26
**Mean substratum size (cm)	15.5	(15.5)	27.6	(27.4)	<.01
*Median substratum size (cm)	12.0		11.0		.72
**Median substratum size (cm)	11.0		17.0		<.01

*Baseflow channel, large boulders excluded.
**Bankfull channel, large boulders included.

TABLE 2. Community measures and relative abundances (%) for the diatom assemblage of each study stream.

	Burned	Unburned
Species richness	34	27
Simpson's index (C)	0.12	0.42
Navicula permitis Hust.	24.7	5.1
Nitzschia dissipata (Kuetz.) Grun.	17.3	4.2
Achnanthes lanceolata (Breb.) Grun.	9.8	1.7
Nitzschia paleacea Grun.	7.6	3.1
Navicula arvensis Hust.	4.8	2.4
Hannaea arcus (Ehr.) Patr.	2.1	63.1

TABLE 3. Means (SD) and *P* values of macroinvertebrate community measures for the study streams.

	Burned	Unburned	*P* value
Density (no./m^2)	9963 (4730)	16,948 (8998)	.31
Biomass (mg/m^2)	1956 (1056)	3198 (1274)	.19
Taxa richness	15.0 (3.7)	20.4 (2.6)	.58
Simpson's index (C)	0.57 (0.09)	0.73 (0.10)	.04

affected watersheds. For example, the Mt. St. Helens eruption of 1980 dramatically changed drainage patterns and river networks, eliminated terrestrial vegetation, and caused major debris flows that scoured stream channels (Wilzbach et al. 1983, Hawkins 1988). However, high spatial variation in the intensity of these major disturbances may occur, causing temporal differences in recovery patterns (Yount and Niemi 1990). In catchments of YNP the relative area burned ranged from <10% to >90% (Minshall and Brock 1991). Further, the degree of alteration of stream habitat was highly correlated with percent of catchment burned (Robinson and Minshall in press).

In the present study significant differences were observed in the benthic habitat of the two streams. The width:depth ratio of the burned stream was greater than that of the unburned stream. Anderson (1992) also observed increased width:depth ratios following major disturbances in streams of the Cascade Mountains. With large boulders included in the measurements, the unburned stream exhibited significantly greater substratum size. Gurtz and Wallace (1984) demonstrated that large substrata could mediate the effects of large-scale disturbances by providing stable habitat for benthic organisms. At the time of sampling, the burned stream did not contain the larger-sized substrata found in the unburned stream. It is probable that the larger substrata in the burned stream were buried by inorganic sediments following the wildfire, as has been observed in other YNP streams (Minshall personal observation). Thus, one effect of the wildfire appeared to be alteration of the substrata in such a manner as to make the benthic habitat more susceptible to future disturbances (e.g., Gurtz and Wallace 1984).

Lamberti et al. (1991) found that faunal densities and macroinvertebrate species richness had recovered within one year following a major debris flow in an Oregon stream. In central Idaho, however, streams disturbed by wildfire and unburned reference streams showed little similarity in macroinvertebrate assemblages, even after five years of recovery (Richards and Minshall 1992). Similarly, in the present study the influence of wildfire was still apparent after five years. Macroinvertebrate community structure was not similar between the two systems, despite their close proximity to each other (0.5 km). Most researchers agree that recovery of the benthic community will correspond to recovery of the surrounding landscape (Steinman and Lamberti 1988, Minshall et al. 1989, Lamberti et al. 1991, Minshall and Brock 1991, Anderson 1992, Richards and Minshall 1992, but see Hawkins 1988).

Primary producers (lotic algae) may recover sooner than consumers (macroinvertebrates and fish) because of their much shorter life cycles, and subsequently they may influence recovery of the higher trophic levels (Steinman and McIntire 1990). In the present study, periphyton biomass (as AFDM) in the unburned stream was 1.7X greater than in the burned stream, implying a present lack of recovery by primary producers in the burned system. Macroinvertebrate taxa richness also was greater in the unburned stream than in the burned stream. How functional or structural recovery of macroinvertebrates is related to algal recovery following wildfire has yet to be determined, but provides an interesting and important avenue for future research. Algae have shorter life cycles and reduced mobility relative to macroinvertebrates, and possibly the two groups respond differently to large-scale disturbances.

TABLE 4. Mean (SD) density and relative abundance of the 10 most abundant macroinvertebrate taxa from each stream. These taxa constituted >90% of the assemblage in their respective streams.

Taxa	Density (no./m^2)	Relative abundance (%)
Burned		
Chironomidae	5437 (2218)	59.7 (19.2)
Simuliidae	2737 (4583)	18.2 (24.1)
Baetis bicaudatus	576 (346)	8.1 (6.3)
Hydracarina	148 (232)	1.5 (2.3)
Epeorus albertae	95 (123)	1.0 (1.2)
Zapada columbiana	90 (72)	1.0 (0.7)
Epeorus longimanus	80 (125)	0.5 (0.7)
Cinygmula	75 (71)	0.8 (0.7)
Rhithrogena	37 (52)	0.3 (0.3)
Ameletus cooki	22 (15)	0.3 (0.2)
Unburned		
Chironomidae	14,676 (8289)	84.7 (6.7)
Hydracarina	372 (253)	2.1 (1.6)
Cinygmula	314 (187)	1.7 (0.8)
Zapada columbiana	310 (215)	1.6 (0.6)
Simuliidae	307 (181)	3.8 (5.3)
Baetis bicaudatus	125 (60)	1.4 (1.7)
Drunella coloradensis	75 (64)	0.4 (0.5)
Rhyacophila angelita	73 (55)	0.4 (0.2)
Rhyacophila tucula	52 (29)	0.3 (0.1)
Kogotus	52 (35)	0.3 (0.2)

After five years of recovery, the channel of the burned stream still appeared unstable as indicated by different diatom assemblages between the two streams. For example, the small, adnate diatom *Navicula permitis* Hust. was predominant in the burned stream but was found in relatively low abundance in the unburned stream. *N. permitis* was predominant in other YNP streams influenced by the 1988 wildfires, and it has been suggested that a diatom community with an abundance of *N. permitis* is indicative of more physically disturbed stream environments (Robinson et al. 1994). Further, Robinson et al. (1994) showed diatom recovery among 14 streams in Yellowstone was inversely related to degree of disturbance by wildfire. Similarly, Steinman and Lamberti (1988) found little recovery, after six years, in the composition of algal communities in intensively disturbed streams of Mt. St. Helens. In summary, benthic community recovery patterns appeared to be related to the recovery of stream physical habitat which, five years after the 1988 wildfires, still displayed evidence of instability. When examining the recovery of benthic communities following large-scale disturbance, one must remain aware of the connections between the terrestrial landscape, lotic habitat, and benthic organisms.

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EFFECTS OF BROWSING BY NATIVE UNGULATES ON THE SHRUBS IN BIG SAGEBRUSH COMMUNITIES IN YELLOWSTONE NATIONAL PARK

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ABSTRACT.—The effects of elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), and mule deer (*Odocoileus hemionus*) browsing on shrubs in big sagebrush (*Artemisia tridentata*) communities were monitored over a 31-year period in Yellowstone National Park. Ungulates were restricting Wyoming big sagebrush (spp. *wyomingensis*) heights, size, and recruitment on the lower-elevation stratum only, while no such suppression was observed on the high-elevation stratum. Parallel increases in mountain big sagebrush (spp. *vaseyana*) densities and cover occurred over the study period on both browsed and unbrowsed sites at the higher-elevation stratum, although big sagebrush, green rabbitbrush (*Chrysothamnus viscidiflorus*), and horsebrush (*Tetradymia canescens*) were slightly taller and crown sizes were slightly larger on unbrowsed than browsed sites. Wyoming big sagebrush utilization (percent leader use) was eight times higher ($\bar{x}$ = 87 ± 7.2% by pronghorns, mule deer, and elk) on the low-elevation winter range stratum (the Boundary Line Area [BLA] portion of the winter range), while mostly mountain big sagebrush with leader use averaged only 11 ± 4.1% (nearly all by elk) on the high-elevation range stratum. In addition, annual aboveground biomass production of big sagebrush did not differ between browsed and unbrowsed study sites on the high-elevation stratum of the winter range. Population turnover was higher on browsed big sagebrush at the high-elevation plots; seedling germination and survival rates were higher on browsed plots versus unbrowsed plots. No difference was observed in percent dieback of big sagebrush adult plants between browsed and unbrowsed plots at the higher stratum. Browsing did not influence the number of leaves or seedstalks per plant (P > .05), but leaves averaged 45% longer and seedstalks 42% longer on browsed big sagebrush. Ungulate browsing, however, apparently suppressed production, germination, and survival of Wyoming big sagebrush on the low-elevation stratum. Numbers of Wyoming big sagebrush declined 43% and cover declined 29%, 1957–1990, on browsed sites on the BLA. Annual biomass production on browsed sites at the low-elevation stratum was only 6–35% that of unbrowsed sites, and big sagebrush recruitment was less on browsed sites. Percent leader use of big sagebrush did not differ between the period of ungulate reductions, 1962–1969, and the 1980s on the lower stratum ($\bar{x}$ = 87% leader use), but utilization was less on higher portions of the winter range during the period of elk reductions ($\bar{x}$ = 2%) than during the 1980s following cessation of elk controls ($\bar{x}$ = 11%).

Key words: big sagebrush browsing, northern Yellowstone elk, pronghorn, mule deer, Cervus elaphus.

Native populations of elk (*Cervus elaphus*), bison (*Bison bison*), and pronghorn (*Antilocapra americana*) were artificially reduced in Yellowstone National Park (YNP), particularly from 1942 through 1967 (Meagher 1973, Houston 1982). Reductions were terminated in 1967 when an experimental management program of natural regulation was initiated (Cole 1971, Houston 1976, 1982). Elk and other ungulate numbers tripled after cessation of controls, and concerns were expressed over high ungulate densities (Chase 1986, Kay 1991). Appropriate numbers of ungulates for the park are unknown since no similar control area exists where wolves (*Canis lupus*) are present and where ungulate migrations are completely unrestricted by humans (Cayot et al. 1979, Peek 1980). Ungulate densities are likely slightly above natural conditions, in that three independent computer models suggest 8–15% fewer elk and 10–25% fewer bison would occupy the system if wolves were recovered (Garton et al. 1990, Boyce 1993, Mack and Singer 1993).

Early workers expressed concern about apparent overbrowsing and declines in big sagebrush (*Artemisia tridentata*) due to possible overabundant populations of elk and pronghorn. As early as the 1930s, Rush (1932) and Cahalane (1943) reported losses of big sagebrush over lower-elevation areas of the northern winter range. Rush (1932) reported that less-palatable rabbitbrushes (*Chrysothamnus* spp.) were increasing. Kittams (1950) concluded that big sagebrush numbers were declining at both lower and higher elevations of the northern winter range. He felt that physical disturbances of big sagebrush by elk during cold periods (shattering and trampling) and an absence of big sagebrush reproduction contributed to the decline. Declines in big sagebrush at the lower-elevation Boundary Line Area (BLA) were attributed by Kittams (1950) to excessive levels of browsing by pronghorn. Park management established a goal to reduce the pronghorn herd by 50% (Kittams 1959); by 1969 pronghorn numbers were artificially reduced from 600–800 to less than 200 through a combination of artificial reductions and severe winters (Barmore 1980).

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Houston (1982) provided alternative interpretations concerning big sagebrush. He reported increases in big sagebrush numbers over all the northern winter range except the BLA near Gardiner, MT, where numbers declined. Houston (1982) compared photos taken during the 1860s to photos retaken in the 1970s. He attributed the increase in big sagebrush at higher elevations to fire suppression and the decline in big sagebrush in the BLA to a return to more natural conditions following the removal of intense grazing by livestock in the early 1930s when the area was added to the park. In 1986 the U.S. Congress directed the National Park Service (NPS) to conduct a study to evaluate whether native ungulates were overgrazing the northern winter range (Congressional Record 1986).

Our objectives were to document trends in big sagebrush abundance on a series of permanently marked plots from 1958 to 1990. Height, canopy size, twig lengths, and annual production of shrubs were compared between browsed and unbrowsed sites.

STUDY AREA

Shrub sampling was conducted on unbrowsed (exclosed) and paired browsed sites at eight ungulate exclosures erected in 1958 and 1962 on Yellowstone's northern winter range. The eight exclosures, 2 ha in size, were located on gently rolling upland steppe ridge and the intervening swale habitats (Fig. 1). We divided the study area into a low-elevation stratum (the BLA of Houston 1982) with two exclosures, and a much larger, high-elevation stratum ($n = 6$ exclosures), based on large differences in ungulate species, elevation, snowpack, precipitation, and big sagebrush subspecies (Fig. 1).

Underlying soils are typic calciborolls, aridic haploborolls, and aridic calciborolls (Lane 1990). Precipitation averages 30 cm at the low-elevation exclosures and 55 cm at the high-stratum exclosures (Houston 1982, Despain 1991). The northern winter range is approximately 1100 km^2 and is located along the upper Yellowstone River drainage. Elevations range from 1500 m at the low-stratum exclosures to about 2200 m at the highest exclosure. The northern winter range is lower, warmer, and drier than the remaining higher plateaus of YNP (Houston 1982). As a result, 80% of the ungulates in the park during winter are found on the northern winter range (Singer 1991).

Dominant shrubs at all the study sites include two subspecies of big sagebrush at the high-elevation stratum, nearly all mountain big sagebrush (*A. t. vaseyana*) with some basin big sagebrush (*Artemisia tridentata tridentata*), while Wyoming big sagebrush (*A. t. wyomingensis*) occurs in the low-stratum study sites. The big sagebrush subspecies vary markedly in their site requirements, growth, and preferences by ungulates (Beetle 1960, Welch et al. 1981, Beetle and Johnson 1982, McArthur and Welch 1982). Rubber rabbitbrush (*Chrysothamnus nauseosus*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and horsebrush (*Tetradymia canescens*) are found at all study sites. *Grayia spinosa* and *Atriplex canescens* occur at the low-stratum study sites (Houston 1982). Dominant grasses are bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), junegrass (*Koeleria pyramidata*), bluegrasses (*Poa compressa*, *P. sandbergii*, or *P. pratensis*), and thick-spike wheatgrass (*A. dasystachyum*; Houston 1982, Wambolt et al. 1987, Despain 1991).

Pronghorn and mule deer occupy only the low-elevation stratum of approximately 52 km^2 within Yellowstone National Park (Barmore 1980, Houston 1982, Singer 1991). About one-half of the pronghorn population also summers in the low-elevation stratum. The lower-elevation (about 1500 m) exclosures are located in typical, nearly snow-free, rolling xeric shrub and mixed grassland habitats. Elk occupy both strata and the entire winter range of 810–1000 km^2 (Houston 1982, Singer 1991). Only elk and bison winter near the high-elevation stratum exclosure sites. Winter snow depths near the higher exclosures (1639–2200 m) are typically 0.4–0.6 m, which are excessive for pronghorn and deer. The abrupt elevation rise for Mt. Everts separates the high and low strata.

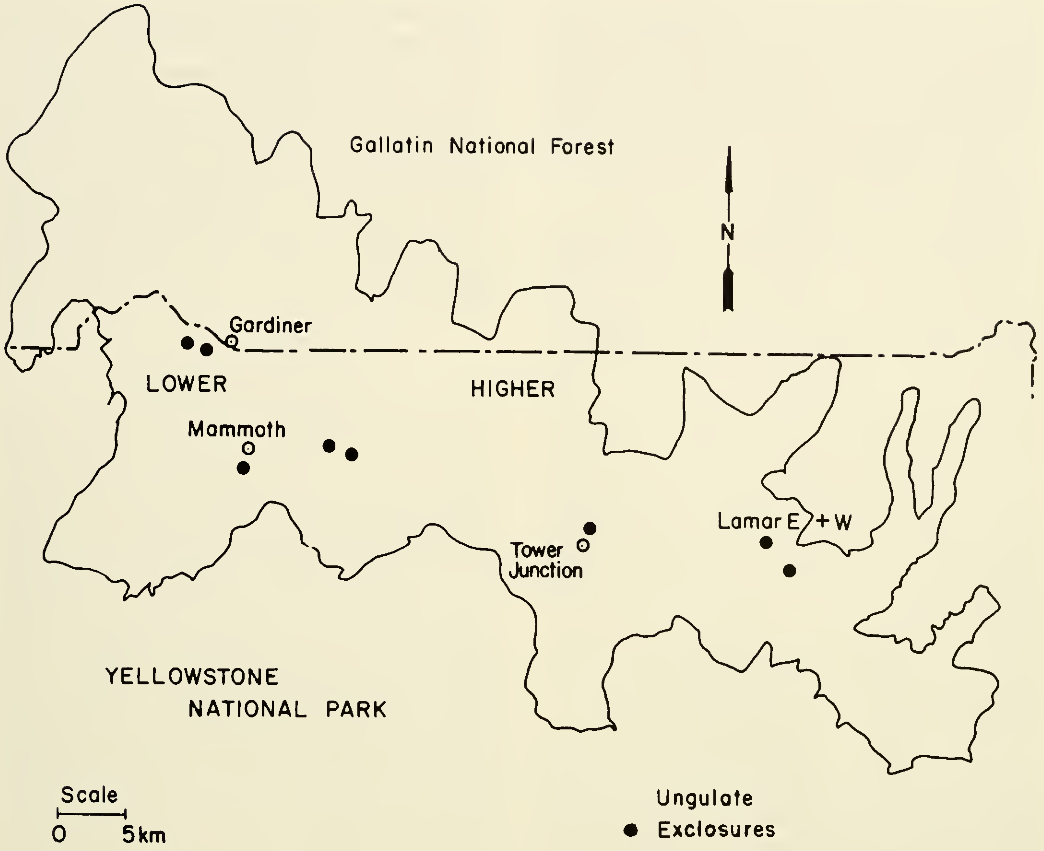

Fig. 1. Map of the northern Yellowstone ungulate winter range and the high-elevation stratum (six exclosures) and low-elevation stratum (two exclosures) big sagebrush study sites. Pronghorn, mule deer, and the Wyoming subspecies of big sagebrush were found only at the low-elevation stratum.

The bison winter range expanded from about 130 km^2 in the 1960s in the higher stratum to about 460 km^2 in the late 1980s during a period of bison population and range expansion (Meagher 1989, Singer and Norland 1995). Periodic bison use of the low-elevation stratum occurred following the population expansion in the late 1980s (Meagher 1989), but vegetation measures reported here are nearly all prior to any bison use of the low-elevation stratum.

Elk numbered about 8000 in 1958–1962 when initial monitoring of the sagebrush belt transects began. Elk were subsequently further reduced by artificial controls to less than 5000 in 1967 (Houston 1982). After cessation of controls, elk steadily increased, with counts ranging from 16,000 to 19,000 from 1982 to 1989 (Singer et al. 1989, Singer 1991). Bison were also artificially controlled until 1967. After cessation of controls, bison on the northern range increased from less than 100 in 1967 to 850 by 1988 (Houston 1982, Meagher 1989). Pronghorn were artificially reduced from 600–800 to <200 (Barmore 1980), and pronghorn numbers remained <200 until about 1981. During the 1980s—apparently due to milder winters—pronghorn increased to about 600 (Singer 1991). Mule deer counts increased from 1000 in 1985 to 2300 in 1988 over the entire deer winter range, the majority of which lies north of the park boundary (Singer 1991). Conversely, mule deer counts just within the park boundaries declined from 230 in the 1960s (Barmore 1980) to about 100 in 1988, in spite of the overall herd increase.

METHODS

Ungulate Densities and Diets

Average ungulate densities near the exclosures were based on actual aerial counts made from fixed-wing aircraft as described in

Barmore (1980), Houston (1982), Meagher (1989), Singer (1991), and Singer and Norland (1995). Densities are uncorrected for visibility bias (Samuel et al. 1988) and therefore represent minimum average densities for the study periods—undoubtedly some animals were missed on the counts (Singer et al. 1989). Diets of all four ungulates found near the study sites on the northern winter range were estimated for each of three winters, December–March 1985–1988, from microhistological analysis of fecal samples (Washington State University, Wildlife Habitat Laboratory, Pullman). Each sample was a composite of 5 g of fresh dung material from 6–12 dung piles. Aggregate average percentages are reported for significant species and plant groups. To avoid confusion between similar species, fresh samples were collected for groups of animals immediately after the groups had vacated an area. Bighorn sheep (*Ovis canadensis*) use steeper terrain on the northern range, and moose (*Alces alces*) are found at higher elevations; neither species was observed near the study sites.

Shrub Utilization Rates

Winter ungulate herbivory rates were sampled on the browsed transects in late winter–spring before leaf emergence (usually late April) in 1963–1969, 1987, 1989, and 1990. Percent twig utilization was obtained from counts of all browsed and unbrowsed twigs on each shrub located in the transect. Diameters at basal point and browsing point were measured on 20 random shoots on every fifth browsed shrub of each species, and bite sizes were estimated following Pitt and Schwab (1990).

Trends in Big Sagebrush, 1958–1990

Five exclosures were erected in 1957 and three more in 1962 ($n = 8$ total). The exclosures were placed in sites representative of mixed big sagebrush/bunchgrass communities. Paired belt transects (each 1.5 m × 30.5 m = 46.5 m^2) were permanently located inside and outside eight of the exclosures (one per exclosure treatment) in big sagebrush communities (Canfield 1941, Parker 1954). Each matched pair of transects was as nearly comparable as possible in terms of slope, aspect, elevation, shrub species, and shrub cover (Barmore 1980, Houston 1982); nevertheless, differences might have occurred. Sampling of transects occurred at the date of exclosure, which should reveal any initial site differences. The transect for exclosure was selected arbitrarily. Heights and species of all shrubs found on the belt transects were recorded in 1958, 1962, 1967, 1974, 1981, 1986, and 1990. Numbers of individual shrubs and any shrub seedlings were tallied. Aerial cover of all shrubs was mapped on graph paper, and shrub cover was later estimated using a grid (Barmore 1980, Houston 1982).

Detailed Site Comparisons in 1986 and 1987

Shrub belt transects were not replicated at a site ($n = 1$ transect per treatment per location, 13 transects total) and were useful primarily for long-term trends and assessment of pretreatment conditions (Parker 1954). In 1986 and 1987 more intensive and better replicated measurements ($n = 15$ plots per treatment) were gathered; 15 circular plots, each 1.7 m in radius (9.3 m^2), were randomly located in big sagebrush stands both inside and outside six exclosures. The tallest height, widest diameter, and perpendicular diameter were recorded for each shrub within each plot. The number of totally dead shrubs was recorded. The percentage of dead material on partially live shrubs was estimated. At every fifth shrub of each species, lengths and diameters of 10 randomly sampled twigs were measured, and every vegetative twig and reproductive stalk were counted. A minimum of 100 twigs of each species from each site was collected, dried, and weighed. Canopy area for each individual shrub was estimated following Peek (1970) from the formula for the area of an ellipse:

$$\text{area} = \left(\frac{\pi}{4}\right) d^1 d^2,$$

where d^1 = largest diameter and d^2 = its perpendicular diameter. All plots and long-term transects were located more than 25 m from exclosure fences to avoid the effects of snowdrifts or ungulate trails along the fences.

Mean shrub height, largest crown area, shoot numbers and lengths, and total shrub cover were compared using a two-way ANOVA, with browsing and exclosure location as treatments. The six exclosures should be considered replications of one treatment (browsing) with 5 d.f. used to test for differences among the treatment and replications. Replications at a location included the 15 random plots in each treatment ($15 \times 2 \times 8$ locations = 240 plots of 9.3 m^2). Nonparametric procedures were used for percent twig utilization comparisons between the 1960s and 1980s and for other data that were nonnormal or with unequal variances (*F*-max tests; Sokal and Rohlf 1981). Frequency distributions of shrubs in browsed and unbrowsed plots were compared using the Kolomogorov-Smirnov test (Zar 1974). All differences discussed are significant at the $P <$ .05 level unless otherwise indicated.

Aboveground biomass production of shrubs was estimated from the numbers of shrubs per plot times the average number of reproductive and vegetative shoots per plant times the average dry weight of shoots. Regression equations for dry weight of shoots (independent variable) were calculated following MacCracken and Viereck (1990) from diameters at base (dependent variable) and length (dependent variable) of shoots. Separate regression equations were calculated for reproductive and vegetative shoots of big sagebrush, green rabbitbrush, and rubber rabbitbrush. The regressions on dry weight were applied to the sample of all twig diameters and lengths to estimate average twig biomass.

RESULTS

Ungulate Densities and Diets

Ungulate densities approximately doubled during the study period on the low-elevation stratum (Table 1), whereas they approximately tripled on the high-elevation stratum during the same period (Table 1). Pronghorn consumed 81% shrubs in their diet, followed by mule deer 50%, elk 8%, and bison 1% (Table 2). Pronghorn diets were 49% big sagebrush, mule deer consumed 23%, and elk diets were only 4%. The higher combined ungulate densities and the presence of pronghorn and mule deer, both of which eat more big sagebrush, suggest that ungulate herbivory on big sagebrush will be greater on the low-elevation stratum study sites. Since pronghorn consume 12x more big sagebrush in their diets than elk and 2x more than mule deer, and since pronghorns also spend summers in the low-elevation stratum, we suspect pronghorn were the most important herbivore on big sagebrush on the low-elevation stratum.

TABLE 1. Average minimum densities of elk, pronghorn, mule deer, and bison near the lower- and higher-elevation exclosures on the northern winter range of Yellowstone National Park. Reported densities are based upon actual counts from fixed-wing aircraft (Houston 1982, Meagher 1989, Singer 1991) and are uncorrected for visibility bias.

	Ungulate density (no./km^2)	
Ungulate	Lower exclosures	Higher exclosures
1965–1968		
Elk	6	6
Pronghorn	3	0
Mule deer	4	0
Bison	0	1
Total	13	7
1985–1988		
Elk	16-19	16-19
Pronghorn	7-10	0
Mule deer	2	0
Bison	tr	2
Total	25-31	18-21

Shrub Utilization Rates

Big sagebrush utilization rates were consistently high (87%) and did not differ between 1963–1969 and 1985–1988 at the low-elevation stratum study sites dominated by the more palatable (to pronghorn) Wyoming big sagebrush (Table 3, Mann-Whitney U tests, $P >$ .05). Pronghorn and elk reductions during 1962–1967 apparently did not result in any decrease in percent leader use of Wyoming big sagebrush on the low stratum. Green rabbitbrush was also used heavily at the low-stratum sites where deer and pronghorn occurred (Table 3). Utilization rates of big sagebrush at the higher sites dominated by mostly mountain big sagebrush, however, increased about sixfold after ungulates increased threefold (Table 3, $P <$ .05). Use of green rabbitbrush did not increase significantly at the high stratum during this period of ungulate increase. Percent leader use of big sagebrush at the lower-elevation sites averaged 87%, but leader use averaged only 11% at the higher sites. Bite sizes averaged 73% of vegetative shoots and 83% of reproductive shoots (n = 180 measured diameters of browsed shoots and 540 unbrowsed vegetative and reproductive shoots). Consumption of annual aboveground biomass of big sagebrush by ungulates averaged about 68% at the low-elevation stratum sites and 9% at higher-elevation stratum sites.

TABLE 2. Mean percent of shrubs in winter diets of four ungulates on Yellowstone's northern winter range, 1985–1988, determined by microhistological analysis of feces ($\bar{x} \pm$ SE).

Ungulate (no. aggregate samples)	Big sagebrush		Rabbit-brush[a]		*Eurotia lanata*		Fringed sage		Total shrubs[b]	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Elk (28)	3.8	3.1	1.6	2.7	0.4	1.0	1.0	2.0	7.8	4.1
Bison (25)	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	1.3	1.6
Mule deer (21)	23.2	15.1	7.2	4.6	0.7	1.0	17.9	16.7	49.7	20.9
Pronghorn (20)	48.7	18.0	5.3	3.5	5.8	6.0	18.5	13.7	80.5	15.7

[a] Rabbitbrush includes *Chrysothamnus nauseosus* and *C. visidiflorus*.

[b] Total shrubs also includes *Populus* spp., *Salix* spp., and *Atriplex* spp.

Big Sagebrush Trends in Densities, Heights, and Cover, 1958–1990

Big sagebrush on belt transects in the lower stratum differed at the time of exclosure in 1958–1962. Densities were similar, but average heights were 50% and cover about 60% those values on transects selected for exclosure (Table 4). Big sagebrush densities, heights, and cover, however, were similar between browsed and unbrowsed transects at the time of exclosure on the high-elevation stratum.

Apparently, ungulates were suppressing Wyoming big sagebrush on the low-elevation stratum during the study period. Wyoming big sagebrush densities decreased 43% and big sagebrush cover decreased 29% on the low-stratum browsed site over the 31-year period (Table 4). Density and cover of Wyoming big sagebrush increased dramatically (350% and 830%, respectively) in the unbrowsed sites of the low stratum. Big sagebrush individuals were taller on unbrowsed sites (Table 4).

Herbivory effects were less on the high-elevation stratum study sites, and all trends were similar for browsed and unbrowsed sites. Mountain and basin big sagebrush density declined, and canopy cover increased on both browsed and unbrowsed belt transects, 1958–1990 (Table 4). Wyoming and basin big sagebrush density declined 39%, but cover increased 39% on browsed sites over the 31 years. Heights of big sagebrush increased on both browsed and unbrowsed sites, but more on unbrowsed sites (Table 4).

Detailed Site Comparisons of Densities, Cover, and Biomass Production in 1986 and 1987

Densities of big sagebrush ($F = 50.9$), total canopy cover of big sagebrush ($F = 8.1$), individual shrub crown area ($F = 22.5$), and heights of big sagebrush ($F = 79.8$, $P < .05$) differed between a much larger sample of browsed ($n = 15$) and unbrowsed plots ($n = 15$ per location, $n = 180$ total) sampled in 1986 and 1987. In each case, however, location was also significant, and the interaction between location and browsing was significant. For example, sagebrush individuals were 59% taller on unbrowsed plots at six exclosure sites, but at the Blacktail exclosures sagebrush plants were taller on browsed plots. Heights of big sagebrush, green rabbitbrush, and horsebrush increased with elevation in both treatments. As a consequence of this exploratory analysis and significant interactions with location, our division of plots into a high and low strata appeared justified, and we analyzed data from the lower and higher study sites separately in all subsequent analyses.

Big sagebrush individuals were shorter and crowns smaller in browsed versus unbrowsed

TABLE 3. Percent of twigs browsed in big sagebrush communities on Yellowstone's northern range. Total ungulate numbers increased twofold at the lower exclosures and threefold at the higher exclosures between 1963–1969 and 1985–1988. The same transects of 46.5 m^2 each ($n = 5$) were sampled both periods; only these five browsed transects were sampled 1963–1969.

Location Shrub species (n = transects)	1963–1969		1985–1988	
	$\bar{x}$	SE	$\bar{x}$	SE
Low elevation ($n = 2$)				
Big sagebrush	88.0	4.2	86.8	7.2
Green rabbitbrush[a]			70.1	10.5
Spiny hopsage[a]			14.8	4.3
High elevations ($n = 3$)				
Big sagebrush	1.9	0.8	11.6	3.5*
Green rabbitbrush	6.7	3.6	8.9	2.9
Horsebrush			46.6	11.4

[a] Only big sagebrush utilization was sampled 1963–1969, and green rabbitbrush at only the higher exclosures.

*$P < .05$, according to Mann-Whitney U tests.

TABLE 4. Changes in density, heights, and canopy cover of individual big sagebrush shrubs between time of exclosure placement in 1958 and 1990 on permanently marked 46.5 m^2 shrub transects, Yellowstone's northern winter range.

	Density of shrubs				Heights (cm)				Canopy cover (m^2/46.5 m^2)			
	1958-1962		1990		1958-1962		1990		1958-1962		1990	
Treatment	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Lower exclosures[a]												
Browsed	21	7	12	2	0.7	0.3	0.5	0.1	19	4	16	4
Unbrowsed	23	15	103	27	1.8	0.6	16.7	0.9	28	7	50	9
Higher exclosures[b]												
Browsed	67	18	41	1.7	1.9	0.9	5.9	1.6	12	2	42	7
Unbrowsed	72	34	37.8	6.2	1.6	0.2	8.6	0.9	10	2	82	9

[a] Big sagebrush subspecies in these transects, mostly *A. t. wyomingensis*, are apparently highly palatable to pronghorns.

[b] Big sagebrush subspecies include mostly *A. t. vaseyana*.

exclosure sites at low elevations ($F = 29.8$, 14.3, respectively), but there was no difference in heights or crown sizes due to browsing at the high-elevation sites ($P > .05$, Table 5). Horsebrush was shorter and crowns were smaller on browsed and unbrowsed exclosure sites at the higher elevations only ($F = 14.5$, 4.6, Table 5). Common rabbitbrush was shorter on browsed plots at the lower elevations, but it was taller on browsed plots at the higher-elevation exclosure sites (Table 5). Density of Wyoming big sagebrush was less on browsed versus unbrowsed plots at the lower exclosures ($F = 14.7$), but there was no effect of browsing at the higher exclosures (Table 6). No difference in the number of dead big sagebrush individuals was observed between browsed and unbrowsed plots at either elevation category ($P > .05$). Twenty-two times more seedlings of the year were observed on browsed than unbrowsed plots at higher elevations ($F = 2.7$, Table 6).

Big sagebrush contributed 82–99% of annual aboveground shrub production in these shrub communities. Browsing did not consistently influence the production of big sagebrush or green rabbitbrush at higher exclosure sites, but browsed rubber rabbitbrush produced less biomass at higher-elevation sites (Table 6). Both Wyoming big sagebrush and rubber rabbitbrush produced much less aboveground biomass on browsed sites on the low study sites (Table 6).

There was no influence from browsing on the number of vegetative or reproductive shoots per shrub for big sagebrush or green rabbitbrush. Reproductive shoots averaged 42% longer (Friedman test, $\chi_r^2 = 38$, $n = 6$ locations, $P < .05$), and vegetative shoots averaged 45% longer on browsed versus unbrowsed big sagebrush (Friedman test, $\chi_r^2 = 42$, $n = 6$ locations, $P < .05$, Table 7). There was no effect of browsing on length of reproductive shoots of green rabbitbrush ($P > .05$).

DISCUSSION

Other studies indicate mountain big sagebrush is preferred and eaten at a higher rate by mule deer and elk than Wyoming big sagebrush, while basin big sagebrush is the least preferred (Sheehy and Winward 1981, Welch et al. 1981, Personius et al. 1987). Our observations initially appear in constrast with this generalization; we observed 70% more winter utilization on Wyoming big sagebrush than mountain big sagebrush. Too few basin big sagebrush occurred on the study sites to draw any conclusions. Our data do not constitute a palatability test, however, in that mountain and Wyoming subspecies did not occur at the same study sites. We suspect pronghorn were the primary herbivore on Wyoming big sagebrush in lower study sites; pronghorn find the Wyoming subspecies highly palatable (Beetle 1960, Beetle and Johnson 1982), and that subspecies was more available to all ungulates due to shallow snows and more winds in the low stratum. Ungulate preference for big sagebrush subspecies also varies between locales (Welch et al. 1981, McArthur and Welch 1982); for example, Dietz and Nagy (1976) found Wyoming big sagebrush was preferred by mule deer in Colorado.

Mountain and basin big sagebrush seedling germination, establishment, and survival were apparently enhanced by browsing and ungulate grazing (possibly due to secondary effects

TABLE 5. Individual shrub crown and heights of shrubs in browsed and unbrowsed (protected) sites on Yellowstone's northern elk winter range. Samples were drawn from (n = 180) plots of 9.3 m^2 each located randomly in browsed and unbrowsed sites in 1986 and 1987.

Shrub species	Crown area (cm^2)				Heights (cm)			
	Unbrowsed		Browsed		Unbrowsed		Browsed	
Location	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Big sagebrush[a]								
Lower (Artrwy)	678	85	347	66*	50	2	37	4*
Higher	798	90	524	51	79	3	71	2
Horsebrush								
Lower	45	7	37	13	15	1	11	2
Higher	575	222	71	93*	63	10	27	3*
Common rabbitbrush								
Lower	287	109	278	85	78	8	43	3*
Higher	196	42	881	590*	59	5	50	11
Green rabbitbrush								
Lower	76	13	104	55	36	11	28	3
Higher	742	70	392	42	79	3	53	2*

*Significant difference between grazed and control means using ANOVA, $P < .05$.

[a] Big sagebrush subspecies included lower exclosures—*A. t. wyomingensis* only; higher exclosures—mixed populations of *A. t. tridentata* and *A. t. vaseyana*, but nearly all *A. t. vaseyana*.

TABLE 6. Estimated annual production (g/m^2) of the most common shrubs in browsed and unbrowsed big sagebrush communities at six exclosures on Yellowstone's northern winter range (n = 15 plots each in both browsed and unbrowsed treatments at each site). Wyoming big sagebrush is found only at the lower-stratum exclosures, and mixed populations of nearly all mountain with some basin big sagebrush at the higher exclosures.

	Lower elevations				Higher elevations			
	Unbrowsed		Browsed		Unbrowsed		Browsed	
Exclosure location	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Estimated biomass (g/m^2)								
Big sagebrush	18		1.9		73.6		72.6	
Green rabbitbrush	0.1		1.5		3.1		5.8	
Common rabbitbrush	0.6		0.3		5.9		4.1	
No. big sagebrush individuals/9.3 m^2								
No. alive	16	2	2	1*	13	2	15	2
No. dead	1.3	0.4	0.6	0.5	3.3	0.8	5.9	1.9
No. seedlings	0.8	0.3	0.2	0.1	0.2	0.1	4.4	1.4*

*$P < .05$ according to t tests. No tests were conducted on biomass since it was estimated from a product of no. of plants × average no. of shoots × average weight of shoots. Tests were conducted on each of those parameters separately, however (see text and Table 7), suggesting statistically significant differences at the lower elevations.

such as reductions of herbaceous vegetation competition and ungulate hoof action) at the higher winter range, but the opposite trend was observed on lower sites. McArthur et al. (1988) also observed more big sagebrush seedlings on a site browsed by mule deer in winter than on an unbrowsed site. The physical act of ungulate grazing, with its accompanying hoof action, greater soil disturbance, more bare ground, and less standing dead vegetation and litter, may provide conditions more suitable to big sagebrush germination. Big sagebrush individuals are smaller on browsed sites, which may also benefit establishment and survival of seedlings due to reduced competition for light, soil moisture, and other resources.

Ungulate herbivory suppressed big sagebrush on the lower-elevation sites, where almost no recruitment of Wyoming big sagebrush occurred on browsed sites; apparently few seedlings survive the intense browsing. Wyoming big sagebrush reproduces more successfully

TABLE 7. Numbers and lengths of reproductive and vegetative stalks on shrubs in browsed and unbrowsed plots in big sagebrush communities on Yellowstone's northern range (n = no. shrubs).

Species Location	No. reproductive flowers/shrub				Length (cm) of flower stalks			
	Unbrowsed		Browsed		Unbrowsed		Browsed	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Big sagebrush								
Lower (Wyoming spp. only)	15	6	13	10	4	0.2	8	0.6**
Higher (basin and mountain spp.)	21	7	17	6	14	0.7	18	0.6**
Green rabbitbrush								
Higher	10	3	16	10	11	0.4	12	0.4
	No. vegetative shoots/shrub				Length (cm) of vegetative shoots			
Big sagebrush								
Lower	99	23	88	18	2	0.1	3	0.4
Higher	83	31	59	12	5	0.5	7	0.5**
Green rabbitbrush								
Higher	33	7	52	20	6	0.2	8	0.4**

*$P < .05$.

**$P < .01$. Differences between numbers in browsed and unbrowsed plots were tested with t tests and lengths with Mann-Whitney U tests.

than the other subspecies on xeric sites (Welch and Jacobson 1988), and the xeric, sodic clay soils of the low stratum are clearly more suitable to Wyoming big sagebrush. At the high levels of ungulate herbivory we observed (roughly 68% biomass removal), the Wyoming subspecies is presently suppressed by ungulates.

The ability of Wyoming big sagebrush to recover from herbivory is less than for mountain and basin big sagebrush. Wyoming big sagebrush is shorter (individuals often do not exceed 0.3 m), seedling growth rates are lower, and current annual growth is less than for the other two subspecies (McArthur and Welch 1982, Booth et al. 1990). The approximately 66% decline in numbers of mule deer using the lower stratum within the park over the past two decades may be due to the localized Wyoming big sagebrush decline. Pronghorn did not decline in the lower stratum during the same period, but pronghorn, unlike mule deer, were artificially reduced well below carrying capacity levels during the 1960s (Houston 1982), and they may still be recovering from the reductions.

Increases in height and cover of big sagebrush are reported after protection from ungulates. Robertson et al. (1970) reported big sagebrush cover increased 76% after 30 years of protection from browsing, although mean heights declined 12%. Heights and crown sizes were similar, but live cover by big sagebrush was greater on unbrowsed sites on a mule deer winter range, primarily due to a greater dieback of browsed big sagebrush (McArthur et al. 1988). Average crown dieback was 64% in the browsed area and 17% in the unbrowsed area (McArthur et al. 1988). Mule deer use was heavy (370 deer-use days/ha), and dieback of big sagebrush occurred after two successive winters of heavy snowfall (McArthur et al. 1988).

Browsing by native ungulates stimulated seedstalks and leaves of big sagebrush and leaves of green rabbitbrush on the study sites. Stagnation of shrubs occurred inside big game exclosures after only two years of exclosure—nonuse of big sagebrush resulted in an average 36% reduction in biomass production over clipped plants (Tueller and Tower 1979). Numbers of sprouts of green rabbitbrush were similarly increased by clipping (30% herbage removal), and new growth was longer, leaves were larger, and leaves remained green for one month longer (Willard and McKell 1978). On the other hand, browsing of more than 80% of the leaders of mountain big sagebrush by mule deer resulted in a reduction of 50–93% in total number of seedstalks per plant and a reduction of 0–53% in length of seedstalks (Wagstaff and Welch 1991). Grazed grasses on the northern Yellowstone winter range have higher protein levels (Coughenour 1991), and grazing stimulates aboveground growth of grasses (Frank and McNaughton 1993). Increased vigor in new growth of browsed shrubs on the Yellowstone northern winter range is consistent with these observations of grasses, and shrub vigor may be the result of increased rates of nutrient cycling due to ungulate defecation and urination (McNaughton 1979). In addition, plant competition is reduced and water availability may be increased on browsed sites on the northern winter range due to smaller crown sizes and fewer transpiring tissues for individual shrubs.

Historic mean duration between fires was 25 years on the Yellowstone northern winter range, but due to fewer fire starts and active fire suppression, no significant burning of grasslands occurred between 1870 and 1988 (Houston 1973, Romme and Despain 1989). Big sagebrush communities had not yet achieved climax postfire state on the northern winter range as indicated by increases in heights and cover of both browsed and unbrowsed big sagebrush individuals between 1958 and 1990. Browsed big sagebrush communities on higher-elevation ranges were replacing themselves; many successful seedlings and small individuals were observed on browsed versus unbrowsed sites. Lomasson (1948) observed almost no reproduction for 40 years in a stand of big sagebrush, but then reproduction increased as the original population began dying. Average life span of big sagebrush is 53–72 years, and in a mature, undisturbed stand, most big sagebrush individuals are in the 55–59-year age class (Roughton 1972). Sagebrush recovery following fire varies from a few years to 30 years depending upon environmental conditions for reestablishment (Sneva 1972, Harniss and Murray 1973). If most big sagebrush communities we studied on the northern winter range last burned in the 1840–1890 period (Houston 1973), then most big sagebrush populations should have approached senescence and population turnover at the time of the 1986–87 sampling.

Ungulate herbivory levels on the lower study stratum restricted growth, establishment, and survival of big sagebrush at the time of this investigation, although browsed big sagebrush communities were stable or increasing at the higher elevation. Suppression of growth and reproduction of plants by increasing native ungulates can result in a new, altered plant-ungulate equilibrium (Sinclair 1977, Caughley 1981). If unnatural (human-caused) concentrations of ungulates cause plant alterations, the situation is not acceptable under NPS policy (U.S. Department of the Interior 1988). Houston (1982) concluded densities of ungulates in the BLA were unnatural and artificially high due to animal avoidance of hunting outside the park. If so, some form of ungulate management—control, encouragement of migrations—is justified on the BLA. Elk and pronghorn reductions in the 1960s, however, did not reduce percent leader use or improve the declining status of big sagebrush in the BLA. Either effective ungulate densities remained the same near the big sagebrush study sites, the ungulate reductions did not go on long enough, or high preference for the Wyoming subspecies by pronghorn maintained high levels of herbivory in the area during the control period.

We caution that we were unable to calculate appropriate or recommended ungulate herbivory levels or ungulate densities for the northern winter range. Our data included two dichotomous periods in ungulate management. The first period of our study, 1958–1968, was clearly a period of ungulate underpopulation during which time elk, bison, and pronghorn were controlled far below ecological carrying capacity (ECC) densities (Barmore 1980, Houston 1982, Boyce 1993, Mack and Singer 1993, Singer and Norland 1995). The second period of our investigations, 1986–1988, likely was a time of ungulate densities in excess of natural conditions, at least for elk and bison. This statement is not based upon any comparisons to control conditions (no similar ecosystem exists with wolves and nondisrupted migrations for a comparison), but upon the conclusions of Houston (1982) that elk concentrations were unnaturally high in the low-elevation BLA stratum, and computer predictions that elk and bison would number 8–25% less following wolf restoration (Garton et al. 1990, Boyce 1993, Mack and Singer 1993). Pronghorn densities in relation to ECC are unknown—one author feels coyotes (*Canis latrans*) are suppressing pronghorn on the northern Yellowstone winter range and that, following wolf restoration, coyotes will decline and pronghorn will further increase (Berger 1991). Wolf restoration occurred on the study area during the winter of 1994–95, providing an opportunity to test the effects of wolves upon ungulate-plant interactions in the Yellowstone ecosystem (Cook 1993).

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SOFT SEDIMENT BENTHIC MACROINVERTEBRATE COMMUNITIES OF THE GREEN RIVER AT THE OURAY NATIONAL WILDLIFE REFUGE, UINTAH COUNTY, UTAH

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ABSTRACT.—Benthic macroinvertebrates from four habitat types (river channel, ephemeral side channel, river backwater, and seasonally inundated wetland) were examined from the Green River at the Ouray National Wildlife Refuge, Uintah County, UT, June–August 1991. Four major taxa (Nematoda, Oligochaeta, Diptera: Ceratopogonidae, and Chironomidae) were quantified. Cluster analysis of densities showed that habitat types with comparable flow conditions were the most similar. Highest to lowest overall benthic invertebrate densities of the four habitats were as follows: ephemeral side channel, river backwater, seasonally inundated wetland, and river channel. Nematodes were the most abundant taxon in all habitat types and sample dates except the August sample of the river channel and river backwater and the July sample of the seasonally inundated wetland.

Key words: benthic macroinvertebrates, Nematoda, Oligochaeta, Ceratopogonidae, Chironomidae, river benthos, wetland, benthos, Green River.

In 1962 Flaming Gorge Dam was completed on the Green River in northeastern Utah. This, in addition to dikes constructed along the river's course and the introduction of nonnative fishes, has altered natural conditions such that many native fishes have reached the brink of extinction and are now listed as endangered species. Grabowski and Hiebert (1989) studied the Green River below Flaming Gorge Dam and noted the importance of backwaters as nursery habitats to introduced and native fishes. They found the most important food items to be benthic macroinvertebrates, predominantly chironomid larvae. Their investigation was confined to two habitats: the main channel and river backwaters. We also studied benthic communities of the river channel and backwater habitats and two additional habitats—seasonally inundated wetlands and ephemeral side channels. No published information exists about the community structure of benthic macroinvertebrates in these latter two habitat types.

Benthic invertebrates of large rivers are poorly known. Difficulty in sampling, the amount of time needed to process samples, identification of specimens after collection, and heterogeneity of habitats make study difficult and often expensive. Studies of riverine systems have utilized divergent methodologies. Some studies randomly sample an entire river cross section and do not attempt to quantify different river habitat types (Grzybkowska 1989, Grzybkowska et al. 1990, Munn and Brusven 1991). Other studies have been directed toward specific river habitats such as riffles (Rader and Ward 1988, Morgan et al. 1991), floodplains (Gladden and Smock 1990), or tailwaters of reservoirs (Swink and Novotny 1985). Relatively few have simultaneously studied multiple habitat types in a single river system (Beckett et al. 1983, Grabowski and Hiebert 1989).

Our purpose was to determine densities and community assemblages of the major benthic macroinvertebrates in four Green River habitats: river channel, ephemeral side channel, river backwater, and seasonally inundated wetland. Benthic samples were taken from June through August 1991, in the Green River at the Ouray National Wildlife Refuge, Uintah County, UT, USA.

STUDY SITES

The Green River originates in Wyoming and flows south through eastern Utah to its confluence with the Colorado River (Fig. 1). It adds more volume to the Colorado River system than any other tributary. In eastern Utah, at river km 404, the Green River enters the Ouray National

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Wildlife Refuge. This section of the river has the lowest gradient of the entire Green River system. Riparian vegetation consists of willow and tamarix with occasional cottonwoods. We collected monthly samples in the Ouray National Wildlife Refuge (see also Fig. 2). In addition to benthic samples, water chemistry was determined for each habitat type on each sample date (Table 1). Salinity and conductivity were recorded with a YSI meter (Yellowstone Instruments); turbidity was measured with a nephelometer; and hardness, pH, and alkalinity were determined with a Hach Kit (Hach Chemical Corporation). Water chemistry was recorded at three locations per sample area on each sample date. At each site, a min-max thermometer was placed near the benthos-water interface at the time of sampling and left for 10 days. Substrate composition was estimated visually.

River Channel

The river channel was sampled approximately 1.3 km north of the United States Fish and Wildlife Service (USFWS) hatchery on the Ouray National Wildlife Refuge. Sampling was adjacent to a sand bar that decreased water turbulence and prevented shifting sands. Water chemistry values were relatively stable. Turbidity was substantially higher during the August sample. Substrate consisted mostly of sand with little silt and detritus. Water levels were too high during June (peak flow) to allow sampling.

Ephemeral Side Channel

During high flows the Green River will occupy various smaller channels that are dry during low-flow intervals. We have named such habitats "ephemeral side channels." The ephemeral side channel studied was approximately 2.75 km south of the USFWS hatchery. For most of the year water levels in the main channel were below the level of the ephemeral side channel. However, during peak flow, water filtered through a wooded area and gathered into the channel, which was 10 m wide and 500 m long. As the river level dropped, flow slowed and eventually stopped. Because the side channel dried up shortly after the July sample, no August sample was taken. Most notable of the water chemistry measurements was the increase of salinity and alkalinity when comparing June to July. Water temperature also deviated more during July. Substrate consisted mostly of firm silt and detritus with little sand. Sediment deposition contributed little to the site during our study.

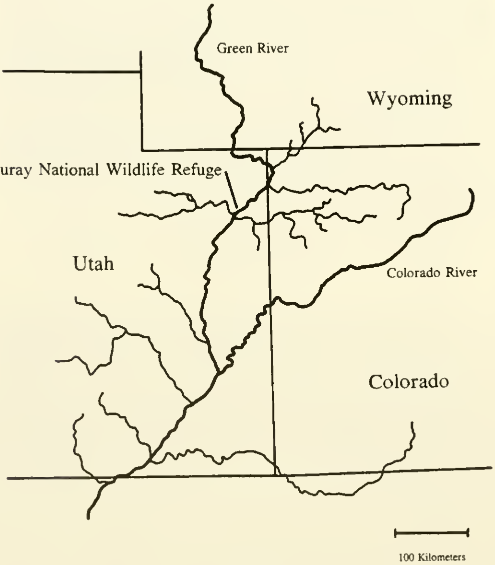

Fig. 1. Regional map showing the location of the Ouray National Wildlife Refuge.

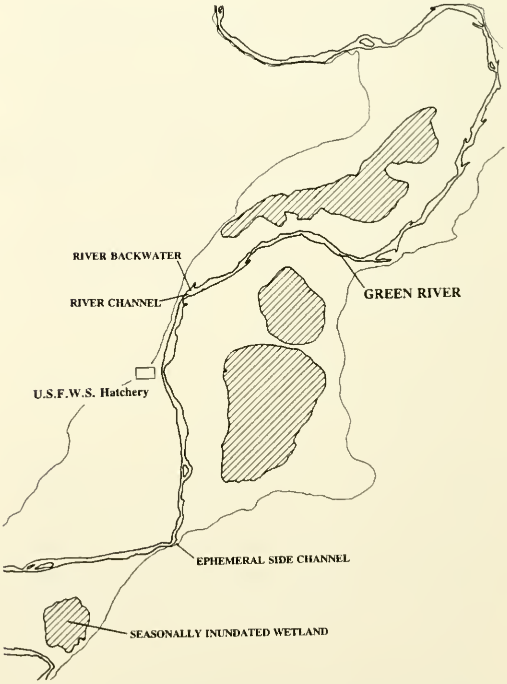

Fig. 2. Local map of the Ouray National Wildlife Refuge, Uintah County, UT, showing the location of sampling sites.

TABLE 1. Mean ± standard deviation water chemistry values from Green River sample sites, June–August 1991 ($n = 3$, temperature in °C, salinity in percent, conductivity in μmhos, turbidity in NTUs, hardness and alkalinity in ppm $CaCO_3$).

Habitat type	Date	Min./max temp.	pH	Salinity	Conductivity	Turbidity	Hardness	Alkalinity
River channel								
	7/15	*	8.14 ± .09	.04 ± .0	753 ± 6	183 ± 318	411 ± 0	183 ± 10
	8/12	20.5/26.5	8.48 ± .10	.04 ± .01	718 ± 8	402 ± 41	320 ± 20	205 ± 17
Ephemeral side channel								
	6/3	20.5/30.5	9.0 ± 0	.03 ± .06	326 ± 10	57 ± 6	183 ± 20	171 ± 0
	7/1	16/30.5	9.14 ± .16	.12 ± .03	445 ± 5	127 ± 21	228 ± 10	240 ± 17
River backwater								
	7/10	20.5/29.5	7.98 ± .23	.01 ± .01	523 ± 23	57 ± 9	228 ± 10	183 ± 20
	8/8	19/26.5	8.59 ± .12	.03 ± .0	730 ± 111	45 ± 11	268 ± 40	228 ± 26
Seasonally inundated wetland								
	6/10	19.5/26.5	9.0 ± 0	.02 ± .0	314 ± 8	52 ± 8	154 ± 0	143 ± 10
	7/12	22/32	8.37 ± .11	.02 ± .01	446 ± 20	36 ± 8	205 ± 0	223 ± 0
	8/15	22/29.5	8.93 ± .1	.01 ± .0	345 ± 13	195 ± 17	171 ± 17	154 ± 0

*Thermometer lost

River Backwater

River backwaters are submerged during high flows and do not emerge as distinct entities until the river drops. For this reason the river backwater was not sampled during peak flow (June). The river backwater we sampled, located just upstream of the river channel site described above, was approximately 10 m wide × 50 m long and 1.3 m deep. Turbidity, alkalinity, and pH were highest during the August sample. Substrate consisted mostly of loose silt and detritus with virtually no sand. Silt and detritus were constantly being deposited during the study period.

Seasonally Inundated Wetland

This site, commonly called "Old Charlie's Wash," is a shallow floodplain wetland managed by the USFWS for waterfowl and is located approximately 4.3 km south of the USFWS hatchery. As the river rises in the spring, water enters Old Charlie's Wash and, at peak flow, retaining structures are put in place to create a 43-ha pond and to prevent the impounded water from receding as rapidly as the river. By early fall the water in Old Charlie's Wash is nearly depleted by seepage and evaporation. Turbidity increased dramatically during the August sample, and conductivity, hardness, and alkalinity peaked during the July sample. Substrate consisted of firm silt, detritus, and sand.

METHODS

Sampling

Samples were collected during the summer of 1991 (Tables 2–5). Initial sampling of the ephemeral side channel and seasonally inundated wetland occurred just after river flow peaked in early June, but samples for the river channel and backwater habitats were not collected because the water level was too high. All four habitats were sampled during July and all but the ephemeral side channel during August. Fifty core samples were taken along a 30-m transect at each site. Each sample was collected with a clear acrylic tube, 450 mm long × 47 mm in diameter (Shiozawa 1985), which was pushed into the substrate to a depth of 60–80 mm. Sediment from each sample was preserved in 5% formalin with rose bengal stain added to aid in sample sorting.

Sample Processing

In the laboratory we washed each sample to separate organisms from sediments using the following procedure. First, the formalin was drained and replaced with tap water. The sample was then gently stirred to resuspend the sediments and poured into a plastic tray (36.5 cm × 31.5 cm × 6 cm) through which a small volume of warm water flowed. The outflowing water, laden with small sand and clay particles, detritus, and benthic invertebrates, was filtered through a 63-μm screen. Larger

TABLE 2. Densities of benthic invertebrates (#/m²) from the Green River, river channel habitat, Ouray National Wildlife Refuge, Ouray, UT.

	15 July 1991		12 August 1991	
Taxon	Density/m² (95% C.L.)	# of samples processed	Density/m² (95% C.L.)	# of samples processed
Nematoda	24,881 (13,107–47,302)	6	2421 (2063–2840)	5
Oligochaeta	3426 (2565–4570)	18	11,182 (7497–16,678)	5
Insecta				
Ceratopogonidae	3608 (2731–4767)	27	13,026 (9316–18,215)	5
Chironomidae	4150 (2798–6155)	5	3516 (2454–5037)	30
Early instars	1037		3016	
Chironomus	346		0	
Cyphomella	0		58	
Lenziella	576		0	
Paramerina	115		0	
Paratendipes	0		96	
Polypedilum	1844		269	
Procladius	115		0	
Psectrocladius	115		0	
Stempellinella	0		58	
Tanytarsus	0		19	

TABLE 3. Densities of benthic invertebrates (#/m²) from the Green River, ephemeral side channel habitat, Ouray National Wildlife Refuge, Ouray, UT.

	3 June 1991		1 July 1991	
Taxon	Density/m² (95% C.L.)	# of samples processed	Density/m² (95% C.L.)	# of samples processed
Nematoda	261,680 (88,934–769,968)	5	302,603 (215,886–424,154)	5
Oligochaeta	2728 (2096–3546)	15	12,796 (10,681–15,329)	5
Insecta				
Ceratopogonidae	0	30	0	5
Chironomidae	2325 (1843–2927)	30	8185 (6385–10,491)	5
Early instars	979		2075	
Chironomus	1134		3112	
Cryptochironomus	0		115	
Cryptotendipes	19		461	
Lenziella	96		1383	
Polypedilum	19		692	
Procladius	0		346	
Tanypus	19		0	
Tanytarsus	58		0	

sediment particles (sands and structural clays) that remained in the plastic tray were periodically examined for specimens. If none were found, the sediments were discarded. Material collected on the screen was stored in 70% ETOH.

Samples sorted were randomly chosen from the 50 samples taken at each site and date. Each sample was placed in glass petri dishes (from one to six dishes depending on the amount of material) and sorted under a dissecting microscope (see Tables 1–4 for number of samples processed). Four major taxa (Nematoda, Oligochaeta, Ceratopogonidae, and Chironomidae) were counted. Only Chironomidae were identified to the generic level. Miscellaneous taxa were also recorded but were not quantified (see Table 5).

The number of samples sorted from each site and sampling date was determined as follows: 5 of the 50 samples were randomly selected and the four major taxa were counted. Because of their contagious distribution (determined by calculating variance to mean ratios), numbers of individuals of each taxon were then log transformed (x + 1). The variance and mean

TABLE 4. Densities of benthic invertebrates (#/m²) from the Green River, river backwater habitat, Ouray National Wildlife Refuge, Ouray, UT.

	10 July 1991		8 August 1991	
Taxon	Density/m² (95% C.L.)	# of samples processed	Density/m² (95% C.L.)	# of samples processed
Nematoda	54,872 (24,350–123,650)	5	134,183 (94,656–190,542)	5
Oligochaeta	26,642 (14,622–48,495)	9	164,731 (101,881–266,728)	5
Insecta				
Ceratopogonidae	96 (90–107)	30	461 (385–552)	30
Chironomidae	31,125 (15,356–63,089)	5	22,863 (12,139–43,136)	6
Early instars	8877		7301	
Chironomus	7032		6340	
Lenziella	346		1249	
Polypedilum	14,179		5860	
Procladius	461		1345	
Psectrocladius	115		0	
Tanytarsus	115		769	

TABLE 5. Densities of benthic invertebrates (#/m²) from the Green River, seasonally inundated wetland habitat, Ouray National Wildlife Refuge, Ouray, UT.

	10 June 1991		12 July 1991		15 August 1991	
Taxon	Density/m² (95% C.L.)	# of samples processed	Density/m² (95% C.L.)	# of samples processed	Density/m² (95% C.L.)	# of samples processed
Nematoda	7133 (4534–11,266)	8	80,694 (38,595–168,713)	5	88,533 (83,125–94,784)	5
Oligochaeta	4573 (3402–6141)	30	87,150 (39,242–193,547)	10	22,249 (11,930–41,494)	5
Insecta						
Ceratopogonidae	0	30	0	14	2478 (1941–3165)	20
Chironomidae	903 (895–915)	30	23,055 (13,707–38,780)	14	3977 (2816–5617)	10
Early instars	96		8769		2479	
Ablabesmyia	0		124		0	
Chironomus	154		41		576	
Cricotopus	19		453		0	
Cryptochironomus	134		206		0	
Cryptotendipes	58		947		346	
Glyptotendipes	58		988		0	
Lenziella	115		1112		0	
Microtendipes	0		1029		0	
Paratanytarsus	231		6505		58	
Polypedilum	19		2388		173	
Procladius	0		124		58	
Psectrocladius	0		41		0	
Tanypus	0		124		173	
Tanytarsus	0		206		115	
Zavrelia	19		0		0	

were used in the following formula to estimate the number of samples to process (Elliot 1977):

$$N = \frac{S^2}{d^2\bar{x}^2}$$

where N = number of samples to process, S = variance, d = level of accuracy desired for the sample (in this case 0.1), and $\bar{x}$ = the mean. For our samples d was chosen to be 0.1, for an accuracy within 10% of the mean. If, after five samples were processed, N was <5 for a specific taxonomic group, no more samples were processed for that group. Those taxa for which N was >5 were counted in an additional sample. The mean and variance for taxa not eliminated were again calculated using the additional sample value(s) and above formula. This process continued until N was less than the number of samples already processed for the taxon. Because of time and financial constraints, we never picked more than 30 samples for any specific habitat and sample date. All sorted samples were preserved in 70% ETOH.

Chironomids were removed from 70% ETOH and placed in distilled water for 10–15 min prior to clearing. Individual specimens were placed in hot (≈80°C) 10% KOH (Cranston 1982) for 5–15 min to clear (larger specimens required more time to clear). After clearing, specimens were transferred to distilled water for at least 5 min. Each specimen was then placed in glycerine on a microscope slide for identification. Only late instars were identifiable. Representative specimens of each genus encountered were permanently mounted. Specimens were classified to the generic level using keys by Mason (1968), Wiederholm (1983), and Merritt and Cummins (1984).

Data Analysis

Average densities (#/m^2) and 95% confidence limits for each of the four main taxa and each genus of Chironomidae were calculated for each sample site and date. Because density distributions were contagious, 95% confidence intervals were calculated for each of the four main taxa using a logarithmic transformation suggested by Elliot (1977; Tables 2–5). These values were then applied to the arithmetic mean (Shiozawa and Barnes 1977). Confidence intervals were not calculated for each genus in the Chironomidae because densities of some genera were too low.

Cluster analysis was performed using the statistical package NTSYS-pc (Rohlf 1992). Several dissimilarity measures, including Bray-Curtis, Canberra's, and Renkonen's, were used to generate distance matrices. A comparison of each of these matrices to the original data showed that the Bray-Curtis measure (Bray and Curtis 1957) provided the best "fit" of the cluster analysis to the data. Average linkage clustering of the Bray-Curtis distances, based on the mean number of individuals/m^2 of each species between habitat types and sample dates, was done with the unweighted pair-group method using arithmetic averages (UPGMA; Krebs 1989).

RESULTS

Invertebrates

Nematodes occurred in every sample processed and were most abundant in the July sample of the ephemeral side channel habitat (302,603/m^2) and least abundant in the river channel August sample (2421/m^2; Tables 2–5). They comprised the majority of benthic invertebrates in all habitats and sample dates except

TABLE 6. Functional group (Merritt and Cummins 1984) and habitat association of Chironomidae genera from the Green River, Ouray National Wildlife Refuge, Ouray, UT.

	Functional group				
Taxon	Collectors	Predators	Shredders	Unknown	Habitat association*
Ablabesmyia		X			SIW
Chironomus	X				RC,ESC,RB,SIW
Cladotanytarsus				X	RC,ESC,RB,SIW
Cricotopus	X		X		SIW
Cryptochironomus		X			ESC,SIW
Cryptotendipes				X	ESC,SIW
nr. *Cyphomella*	X				RC
Glyptotendipes	X		X		SIW
Microtendipes	X				SIW
Paramerina				X	RC
Paratanytarsus				X	SIW
Paratendipes	X				RC
Polypedilum	X	X	X		RC,ESC,RB,SIW
Procladius	X	X			RC,ESC,RB,SIW
Psectrocladius	X		X		RC,RB,SIW
nr. *Stempellinella*				X	RC
Tanypus	X	X			ESC,SIW
Tanytarsus	X				RC,ESC,RB,SIW
Zavrelia	X				SIW

*RC = river channel, ESC = ephemeral side channel, RB = river backwater, SIW = seasonally inundated wetland.

the August river channel and river backwater habitats and the July wetland sample.

Oligochaetes were present in all habitat types and on all sample dates. Densities ranged from a low of 2728/m^2 in the June ephemeral side channel sample to a high of 164,731/m^2 in the July river backwater sample (Tables 2–5).

The lowest abundance of Ceratopogonids was observed in the July river backwater sample (96/m^2). Their density was 136X greater in the river channel August sample (13,026/m^2; Tables 2–5). Ceratopogonids were absent from both June and July samples of the seasonally inundated wetland and the ephemeral side channel.

Ninteen chironomid genera were collected during this study. Fourteen genera were found in the July seasonally inundated wetland samples, and five genera occurred in the August river channel and river backwater samples. Seven genera occurred in only one habitat or on only one date. Six genera were found in the seasonally inundated wetland habitat only, and four occurred only in the river channel. No chironomid genus was unique to the ephemeral side channel or the river backwater. The genus *Polypedilum* was collected in all habitat types and on all sample dates. Total chironomid densities were least (903/m^2) in the June sample of the seasonally inundated wetland and greatest (31,125/m^2) in the July river backwater sample (Tables 2–5). Unidentifiable early instars were collected in all habitat types and in all sample periods and comprised 86% of the river channel sample in August. The most common functional group category of the Green River chironomids was collectors followed by predators and shredders. Specific functional group and Green River habitat association for each genus are presented in Table 6.

Other insects found in the samples are listed in Table 7. Density estimates would not be valid for these taxa because of their ability to avoid the core sampler.

Cluster Analysis

The UPGMA cluster analysis of the benthic invertebrate communities in each habitat type and sample date indicated that sites with similar flow conditions tended to cluster together (Fig. 3). A matrix comparison of original distances calculated using the Bray-Curtis coefficient with distances implied from the dendrogram is presented in Figure 4. Correlation between the two was high ($R = .907$), implying that the dendrogram is an accurate representation of

TABLE 7. Other insects encountered in the Green River ecosystem, June–August 1991.

	River channel		Ephemeral side channel		River backwater		Seasonally inundated wetland		
Taxon	July	August	June	July	July	August	June	July	August
Coleoptera									
Hydrophilidae (larvae)							X		
Diptera									
Chironomidae (pupae)		X			X	X	X	X	
Empididae (larvae)				X		X			
Simuliidae (larvae)		X							
Ephemeroptera									
Baetidae									
Baetis (nymph)		X			X	X		X	X
Callibaetis (nymph)					X				
Caenidae									
Caenis (nymph)				X	X			X	
Tricorythidae									
Tricorythodes (nymph)	X								
Hemiptera									
Corixidae		X			X	X			
Odonata									
Coenagrionidae									
Ischnura (nymph)								X	X
Gomphidae (nymph)		X							
Plecoptera									
Perlodidae (nymph)									
Isoperla	X								

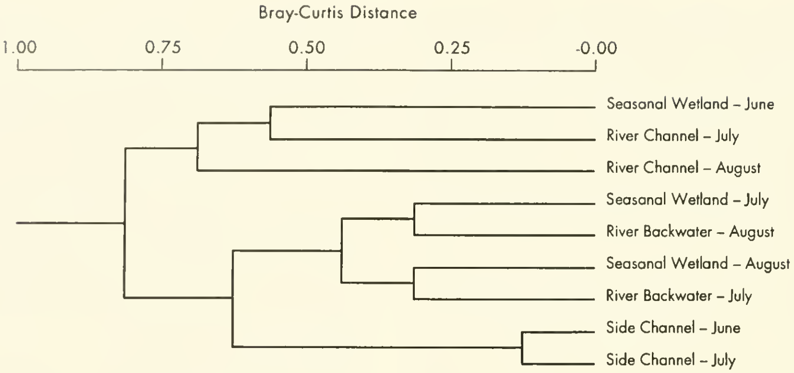

Fig. 3. UPGMA cluster analysis of Green River habitat types located in the Ouray National Wildlife Refuge.

the original Bray-Curtis distances. Ephemeral side channel samples show the greatest similarity (least distance), and wetland and backwater sites are more similar to one another.

DISCUSSION

Nematoda

The importance of free-living nematodes in aquatic systems has not been extensively studied. Aquatic nematodes are known to be microbotrophic, predaceous, and/or parasitic during one or more of their life stages (Poinar 1991). Due to the scarcity of adequate keys and their small size, nematodes are seldom listed beyond the phylum designation in most studies and may not even be quantified. In studies of aquatic systems where nematodes are quantified, highest densities have been found in lakes. Strayer (1985) and Nalepa and Quigley (1983) reported that nematodes comprised 60% and 80%, respectively, of all benthic metazoans in Mirror Lake, NH, and in Lake Michigan with means of 680,000/m^2 (Mirror Lake) and 260,000/m^2 (Lake Michigan). In contrast, Palmer (1990) in Goose Creek and Gladden and Smock (1990) on the floodplain of Colliers Creek reported that nematodes comprised a much smaller percentage (6% of total invertebrates) and occurred at diminished densities (1000–15,000/m^2 and 1746/m^2, respectively) in lotic systems.

In our study nematode density estimates from the seasonally inundated wetland June sample (7133/m^2) and the July and August river channel samples (24,881/m^2 and 2421/m^2, respectively) are comparable to densities previously reported from lotic systems (Gladden and Smock 1990, Palmer 1990). Density estimates for all other sites and dates (54,872–302,603/m^2) are more similar to densities in lentic habitats (see above). Greater densities are achieved in the more stable benthic environments provided by calmer waters and finer sediment particle size. In their study of White Clay Creek, Bott and Kaplan (1989) found that nematode densities were greater in silt than in sand. In our study the highest densities are also associated with a low sand content in the substratum. Low densities reported for the June sample of the seasonally inundated wetland site reflect the relatively short time that water had been on the sample site. Of the four major invertebrate groups collected in this study, nematodes accounted for 8% of the individuals in the river channel August sample and 98% in the June ephemeral side channel. Nematodes accounted for 67.7% of all organisms observed. Palmer (1990), using a 3.3-cm-dia. core and 44-μm mesh, reported that nematodes constituted only 4–15% of the Goose Creek community, with a mean of 9%. Her data are similar to our river channel values. High nematode densities and their high percentage of the total invertebrates that we report from the ephemeral side channel, river backwater, and seasonally inundated wetland are unusual and should be compared to samples taken at similar locations in this and other large rivers using comparable methods.

Oligochaeta

Freshwater oligochaetes are a well-studied and diverse group found in every type of estuarine and freshwater habitat. They feed mostly on bacteria living in soft sediments (Brinkhurst and Gelder 1991). The amount and quality of

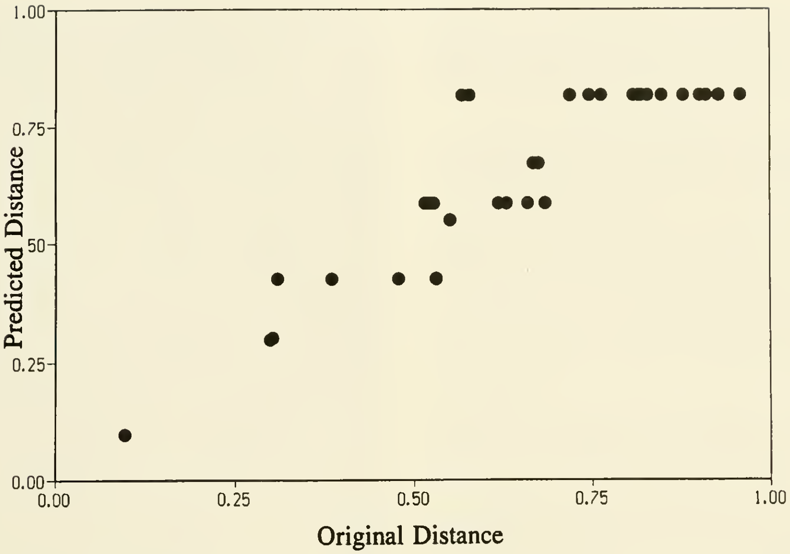

Fig. 4. Comparison of original dissimilarity matrix and implied matrix from the dendrogram.

organic matter found in the sediment are primary factors determining which species will be present in a particular area (Brinkhurst and Cook 1974). We identified our specimens only to class level. Oligochaete densities in nonpolluted lakes are lower than those in organically polluted waters. Densities in Mirror Lake ranged from 30,000 to 33,000/m^2 (Strayer 1985). Jonasson and Thorhauge (1976) reported oligochaete densities in Lake Esrom, Denmark, of 6000–12,000/m^2. Brinkhurst and Cook (1974) found that densities of the three most common tubificids in the more polluted areas of Toronto Harbor ranged from 51,000 to 197,000/m^2. Oligochaete densities in nonpolluted lotic systems tend to be lower. Grzybkowska and Witczak (1990) report oligochaete densities in the lower Grabia River, Poland, ranging from 110 to 900/m^2, and Palmer (1990) reports densities from 5000 to 15,000/m^2 in Goose Creek, VA. Densities from polluted lotic systems can approach 200,000/m^2 (Koehn and Frank 1980).

Oligochaete densities in the seasonally inundated wetland June sample (87,150/m^2) and river backwater August sample (164,731/m^2) are comparable to values observed in polluted systems described above. Densities from both ephemeral side channel samples (2728 m^2 and 12,796/m^2) and both river channel samples (3426/m^2 and 11,182/m^2) are comparable to those in Goose Creek (Palmer 1990). In general, oligochaete densities in our study were higher in habitats with the least amount of water flow (seasonally inundated wetland and river backwater habitat types). Terrestrial vegetation invades wetlands during dry periods, and when the water returns the following spring, decaying vegetation forms a rich food base. Backwater habitats retain fine particles, including detritus, being transported by the river; as summer progresses, this creates an enriched food base. These factors are the likely reason for the convergence oligochaete densities in these two habitats with those in organically polluted systems.

Ceratopogonidae

The study of ceratopogonids has mainly centered on adults because of their economic importance (Davies and Walker 1974). Larvae inhabit a variety of habitats including tree holes, leafpacks, and pitcher plants, but are usually most numerous in shallow areas of streams, lakes, and ponds (Bowen 1983). Aquatic forms are mostly predaceous (Merritt and Cummins 1984), but several species are known to consume algae and plant debris (Kwan and Morrison 1974).

Corkum (1990) investigated streams associated with different land-use types in southwestern Ontario and found densities of 50/m^2 in "forested" sites, 480/m^2 in "mixed" sites, and 5300/m^2 in "farmland" sites. Adamek and Sukop (1992) found maximum densities of only l/m^2 on over-flooded meadows in Czechoslovakia. In Lake Norman, NC, Bowen (1983) reported a mean larval ceratopogonid density of 767/m^2.

Ceratopogonid densities reached a peak in the August river channel sample (13,026/ m^2)—much higher than any reported in the literature above. In their study of the Green River, Grabowski and Hiebert (1989) did not report densities, but did conclude that ceratopogonids were more abundant in river channel samples than in backwaters. Our study supports this conclusion. Average densities for the river channel July and August samples were 3608/m^2 and 13,026/m^2, respectively, compared to 96/m^2 and 461/m^2 for the backwater July and August samples. Ceratopogonid larvae were completely absent from the ephemeral side channel as well as the June and July seasonally inundated wetland samples.

Chironomidae

Chironomidae are typically the most abundant macroinvertebrates in lentic (Strayer 1985) and lotic (Grzybkowska and Witczak 1990) systems. Studies of relatively small geographical areas have reported impressive numbers of species. For instance, Douglas and Murray (1980) found 142 species in Killarney Valley, Ireland. High diversity of chironomids makes them important as indicators of environmental condition (Wingard and Olive 1989). They are also abundant and provide an important food source for fish (Brown et al. 1980, Winkel and Davids 1987, Grabowski and Hiebert 1989), waterfowl (Titmus and Baddock 1980), and other migratory birds (Bowman 1980).

We identified 19 chironomid genera from our sites within the Green River ecosystem. Other investigations of lotic systems have yielded similar numbers—12 genera in the upper Tuscarawas River, OH (Wingard and Olive 1989), 24 genera in the River Frome, England (Pinder 1980), 25 genera in the Mississippi River (Beckett et al. 1983), and 36 genera in Juday Creek, IN (Berg and Hellenthal 1991). Grabowski and Hiebert (1989) studied the Green River in the same general area considered in our study and also identified 19 genera. However, only seven of the genera reported by the latter authors were found in our study: *Chironomus*, *Cricotopus*, *Cryptochironomus*, *Polypedilum*, *Procladius*, *Tanypus*, and *Tanytarsus*.

Densities of chironomids in aquatic systems can vary substantially. In a study of Lake Vissavesi, Finland, Paasivirta and Koskenniemi (1980) reported densities of 64/m^2 in a coarse debris habitat and 2997/m^2 in a moss-grown site. Jonasson and Lindegaard (1979) reported 59,000/m^2 from Lake Myvatn, Iceland. Variability in lotic systems has also been documented. Pinder (1980) reported densities from a low of 48/m^2 to 6273/m^2 in a chalk stream in England, and Grzybkowska (1989) found 10,664/m^2 in the River Grabia, Poland. While no distinct trends exist when comparing chironomid densities in lentic and lotic systems, densities are influenced by sediment size (Paasivirta and Koskenniemi 1980, Beckett et al. 1983).

Chironomid densities from the July and August river channel samples were 4148/m^2 and 3516/m^2, respectively. River backwater samples were 31,125/m^2 and 22,864/m^2 for the same times. Grabowski and Hiebert (1989) reported maximum chironomid densities in the same area of the Green River of less than 100/m^2 for the river channel and 2800/m^2 for river backwaters—substantially less than our estimates. It is possible that annual differences in seasonal discharge, area of the sampling device, and later sampling period all contributed to this discrepancy. However, because of significant differences in mesh size (63-μm ours, 600-μm Grabowski and Hiebert's), data of Grabowski and Hiebert and ours cannot be considered equivalent. It is worth noting that mesh sizes larger than 100 μm have been shown to negatively bias density estimates (Strayer 1985).

Community Similarity

Cluster analysis of the data showed that, in general, habitat types clustered together independent of sample date, suggesting that the different habitat types studied in the Green River are distinct. Beckett et al. (1983), for example, studied five habitats in the Mississippi River and also found them to remain compositionally distinct regardless of flow and sample date. Distribution and abundance of benthic macroinvertebrates characteristic of these habitat types have been attributed to flow conditions and sediment size in our study. Since flow conditions are the major determinant of particle size, flow conditions are likely the determining factor. This conclusion has also been reached by other investigators (Beckett et al. 1983, Statzner and Higler 1986).

Grabowski and Hiebert (1989) concluded that benthic macroinvertebrate densities in backwaters of the Green River were higher than those of the river channel. Our data suggest that the seasonally inundated wetland and ephemeral side channel are also valuable habitats and have the potential to contribute substantial biomass to the Green River system. Oligochaete and chironomid densities reported in our study are comparable to other lotic systems (Koehn and Frank 1980, Pinder 1980, Grzybkowska 1989, Grzybkowska and Witczak 1990, Palmer 1990). High densities of nematodes and ceratopogonids imply that these groups may be very important in the overall energetics of the Green River system. Both should be studied more intensely. The overall dynamics of these communities is undoubtedly associated with seasonal changes in flow as well as year-to-year variability in annual discharge. This study, while describing a backwater, river site, side channel, and floodplain wetland over a short time interval, does not allow a full assessment of either annual or spatial variability. It is clear that some sort of successional colonization of various habitats occurs; for instance, floodplain wetlands are maximum in extent during highest spring–early summer flows, but their faunal development lags peak flooding. Backwaters do not exist during high flows, but as floodplains diminish with receding water levels, backwater habitats develop. Again their faunal assemblages tend to lag behind the emergence of recognized backwaters. While we documented what appears to be seasonal succession within habitat type, such changes should not be assumed the norm. Until a detailed study is undertaken for the Green River or Colorado River system with replicate habitats over at least a full year period, our observations must be considered tentative. Further, annual discharge can vary tremendously from year to year, depending upon factors such as drought cycles and their link with El Niño dynamics in the Pacific. Thus, what is seen in one year may not be representative of all years. Such factors introduce additional variables that should be considered when attempting to understand the dynamics of the benthos of the Green River.

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ALPINE VASCULAR FLORA OF THE TUSHAR MOUNTAINS, UTAH

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ABSTRACT.—The Tushar Mountains of southwestern Utah rise to a maximum elevation of 3709 m, with timberline and krummholz reaching maximum elevations of 3438 m and 3566 m, respectively. Voucher specimens were collected from the alpine region during eight field seasons to inventory this largely unknown alpine flora. Listed are 171 vascular plant species from 102 genera and 34 families that occur in eight types of plant communities within an alpine area of about 19.3 km^2. The seven largest families are Asteraceae (29 species), Poaceae (20), Brassicaceae (13), Rosaceae (12), Cyperaceae (11), Caryophyllaceae (10), and Fabaceae (8). Thirteen species are restricted to the alpine area. The perennial herb growth form accounts for 86.4% of the flora, 5.9% of the species are shrubs, and the remaining species are annuals to short-lived perennials. Bedrock in the alpine region is entirely of Tertiary igneous origin. Vegetation cover and species richness are highest on an andesite ash-flow tuff and latite flow and lowest on hydrothermally altered intercaldera rhyolites and tuffs. Forty-four species (26.0% of the indigenous flora) also occur in the Arctic, and 13 species are at a southern margin of distribution. Eight taxa (4.7% of the flora) are local or regional endemics. The majority of the alpine species appear to have migrated to the range by way of the contiguous mountain system to the north; statistical comparison with neighboring alpine floras shows the flora to be most similar to the floras of the Wasatch Mountains, Uinta Mountains, and Teton Range, with Sorensen's similarity indices of 52.8, 50.2, and 48.8% respectively.

Key words: Utah, Colorado Plateau, Tushar Mountains, alpine vascular flora, alpine vegetation, plant geography.

The Tushar Mountains, located in southwestern Utah in the High Plateaus section of the Colorado Plateau at the eastern margin of the Great Basin (Fig. 1), reach a maximum elevation of 3709 m at the summit of Delano Peak. This elevation is surpassed within the state only by peaks in the Uinta Mountains and La Sal Mountains. A diverse alpine environment and flora occur on the 11 peaks that rise above the elevation of timberline. The alpine area is isolated. Though minor patches of alpine vegetation occur on the Fish Lake Plateau 66 km to the northeast and Markagunt Plateau 81 km to the south, the nearest extensive alpine area occurs in the Wasatch Mountains (Mount Nebo) 157 km to the north. The purposes of this paper are to document this isolated alpine flora, briefly describe the alpine plant communities, and determine possible migrational pathways to the Tushars by means of statistical and qualitative comparisons with neighboring alpine areas.

STUDY AREA

The Tushar Mountains have a length of 60 km and a width of 36 km at the widest point. Vertical relief exceeds 2000 m, with a low elevation of 1695 m at the confluence of Clear Creek and the Sevier River. The range is located within an area of large-volume Tertiary (Oligocene to Miocene) volcanic activity known as the Marysvale volcanic field and is composed mostly of volcanic rocks (Cunningham and Steven 1979). Structurally, the range consists of a plateau-like, north-trending, up-faulted block bordered by structural valleys formed from down-faulted blocks; the High Plateaus section is thus structurally transitional between the Basin and Range Province and the Colorado Plateau Province (Hunt 1987). The major faulting that produced the current linear ranges of the High Plateaus occured between 8 million and 5 million years ago (Steven et al. 1984).

Topography and soil development in the alpine area are strongly influenced by the two volcanic formations exposed near timberline and above (Fig. 2). The mostly plateau-like to domelike ridges in the southern and eastern portions of the alpine region (including Delano Peak) are composed of calc-alkaline basaltic andesite flows and tuffs of the Bullion Canyon Volcanics (Cunningham et al. 1983) on which two soil complexes consisting of mollic cryoborolls, argic pachic cryoborolls, pachic

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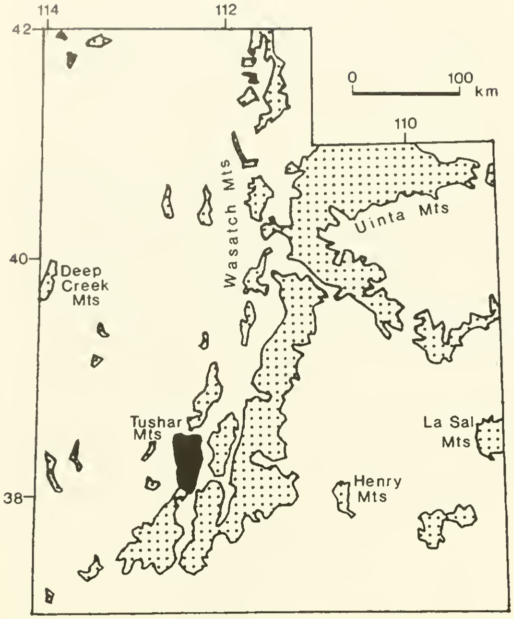
114
112
42
0 100 km
110
Wasatch Mts
Uinta Mts
40
Deep Creek Mts
Tushar Mts
La Sal Mts
Henry Mts
38

Fig. 1. Map of Utah showing location of Tushar Mountains (in black) and other mountainous areas above 2286 m in elevation (generalized and adapted from Smouse and Gurgel [1981]).

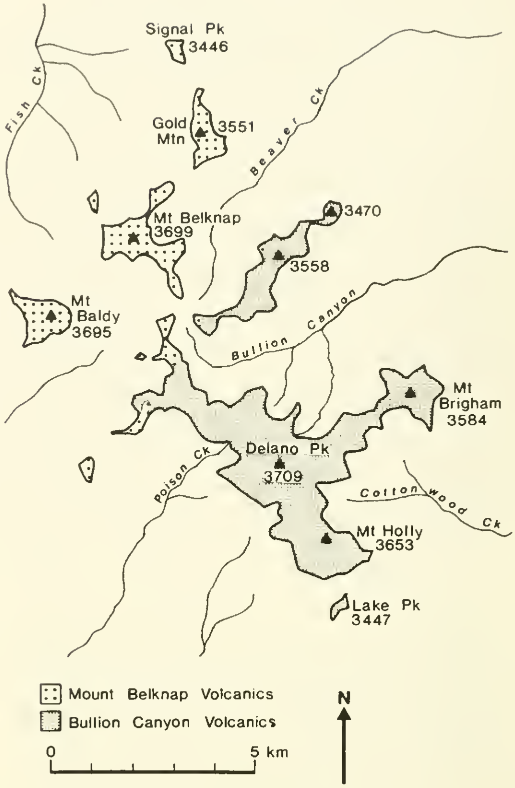
Signal Pk 3446
Fish Ck
Gold Mtn 3551
Beaver Ck
Mt Belknap 3699
3470
3558
Mt Baldy 3695
Bullion Canyon
Mt Brigham 3584
Poison Ck
Delano Pk 3709
Cotton wood Ck
Mt Holly 3653
Lake Pk 3447
Mount Belknap Volcanics
Bullion Canyon Volcanics
0 5 km
N

Fig. 2. Map of the central Tushar Mountains with outlined portions approximating the areas above 3383 m in elevation. Location of igneous formations is generalized from Cunningham et al. (1983).

cryoborolls, lithic cryoborolls, and rock outcrops are recognized (U.S. Forest Service 1993).

The more mountainous northern and western portions of the alpine region are composed of intercaldera siliceous alkali rhyolite lava flows, lava domes, and ash-flow tuffs of the Mount Belknap Volcanics which have been hydrothermally altered in many places (Cunningham and Steven 1979) and which are resistant to weathering. The summit pyramids of Mount Belknap (3699 m) and Mount Baldy (3695 m) consist of steep talus slopes and cliffs; portions of these talus slopes lack a cliff at their head and thus appear by definition (Washburn 1979) to be block slopes formed from periglacial frost action. Soil development in this region is limited to areas too small to map, and all alpine exposures of this formation as mapped by Cunningham et al. (1983) are classified by soil scientists as a cirqueland-rubbleland-rock outcrop complex (U.S. Forest Service 1993).

Pleistocene glaciers produced several well-defined cirques on the eastern side of the crest where glacial ice descended to a low elevation of about 2500 m (Callaghan 1973). Glaciation also occurred on the western side of the crest as evidenced by glacial striations in the Poison Creek drainage. Periglacial patterned ground in the form of stone stripes, stone circles, and stone nets occurs on the main ridgecrest between the elevations of 3432 and 3600 m.

Climate of the Rocky Mountain alpine zone is characterized by Billings (1988) to have a mean temperature of less than 10°C for the warmest month. Climatic data are unavailable for the alpine area in the Tushar Mountains. A weather station located in an Engelmann spruce (*Picea engelmannii*) community 3.6 km south of the alpine region at an elevation of 3136 m has a mean annual temperature of 1.7°C, the warmest months being June, July, and August with mean monthly temperatures of 9.2, 11.7, and 10.9°C, respectively (three years of records). Most of the mean annual precipitation of 909 mm (12 years of records) falls as snow. Rainfall from summer thunderstorms is highest in August, with an average of 74 mm, while the months of June and July receive averages of 46 and 45 mm, respectively (Soil Conservation Service 1993).

An alpine region is defined by Bliss (1985) to be the area above the climatic limit of upright tree growth, although it may include patches of krummholz. The average elevation of timberline in the Tushar Mountains occurs at about 3383 m (11,100 ft), with a corresponding alpine area of about 19.3 km^2 above this elevation. This alpine area, located between 38°20′04″ and 38°27′47″ North latitude and 112°19′32″ and 112°26′42″ West longitude, extends from Signal Peak in the north to Lake Peak at the south over a distance of 14.5 km. Much of the alpine area, centered about 25 km ENE of the city of Beaver, is accessible by Forest Service road 123, which crosses the crest of the range at an elevation of 3505 m.

Timberline coincides with the upper limit of continuous forest and reaches a maximum elevation of 3438 m on a minor ridgecrest on the western (windward) side of the range. Timberline occurs as low as 3341 m on lower ridges and is edaphically depressed even lower on some talus slopes. Engelmann spruce and limber pine (*Pinus flexilis*) are the only arboreal species found at timberline. Subalpine fir (*Abies lasiocarpa*) and aspen (*Populus tremuloides*) approach timberline with maximum known elevations of 3365 and 3292 m, respectively. The krummholz limit, consisting of Engelmann spruce, occurs at about 3566 m on the steep, south-facing slope of Mount Baldy; this slope is protected from prevailing winds by a ridge extending southwesterly from the summit.

METHODS

Voucher specimens were collected from 1984 through 1993 from throughout the range in preparation of a checklist of the vascular plants of the Tushar Mountains. Collected specimens were deposited in the herbarium of Brigham Young University and a search was made in this herbarium for other pertinent specimens. The total known flora for the range consists of 971 taxa representing 924 species, 381 genera, and 89 families (Taye 1994). The alpine region was visited during the same period except for the years 1986 and 1989. Only those species found above local timberline are included in this study.

Species nomenclature and life form classification follow Welsh et al. (1993).

Sorensen's Index of Similarity (Mueller-Dombois and Ellenberg 1974) was used to compare the alpine flora with neighboring alpine floras to determine possible migrational pathways to the Tushars. Differences in nomenclature among the floras were largely resolved with the references of Dorn (1988), Weber and Wittmann (1992), and Welsh et al. (1993). Subspecific taxa were not used in statistical comparisons.

ALPINE VEGETATION

Eight types of alpine plant communities were recognized based on qualitative observations; future intensive study of the vegetation will likely expand this classification. As noted for alpine communities in the Uinta Mountains (Lewis 1970), boundaries between plant communities are usually diffused.

CUSHION PLANT.—Low-growing species dominate the windswept ridgecrests where soils are shallow and outcrops of bedrock and rubble formed in place by frost-heaving are common. Dominant species include *Carex elynoides, Cerastium beeringianum, Erigeron compositus, Festuca ovina, Geum rossii, Phlox pulvinata,* and *Silene acaulis.*

DRY MEADOW.—The warmer and drier south- and west-facing slopes are characterized by a plant cover in which bare soil is generally present between individual plants; rock cover is frequently high and soil disturbance from pocket gophers is common. Spruce krummholz is common at lower elevations. Common species in this extensive community type include *Achillea millefolium, Astragalus miser, Carex elynoides, Castilleja parvula, Cymopterus lemmonii, Elymus trachycaulus, Haplopappus macronema, Helenium hoopsii, Phlox pulvinata, Potentilla glandulosa, P. gracilis, Poa secunda,* and *Ribes montigenum. Geum rossii* occurs occasionally in usually mesic microhabitats. Alpine populations of *Gentiana parryi, Juniperus communis, Sambucus racemosa, Thalictrum fendleri,* and *Viola nuttallii* occur only in this community type at low elevations.

MESIC MEADOW.—Plant cover is generally higher on suitable (nontalus or bedrock) north- and east-facing slopes and near drainage bottoms and is occasionally carpet-like where sufficient soil development has occurred. Alpine avens (*Geum rossii*) is perhaps the most common species in this community. Komarkova

(1979) found this species to be most abundant on slopes with deep soil profiles and moderately prolonged snow cover. Other common species in this extensive community type include *Arenaria obtusiloba, Artemisia scopulorum, Carex heteroneura, Cerastium beeringianum, Erigeron simplex, Luzula spicata, Pedicularis parryi, Phlox pulvinata, Poa reflexa, Polygonum bistortoides, Salix arctica, Saxifraga rhomboidea,* and *Silene acaulis.*

WET MEADOW.—A few wet meadows occur adjacent to rivulets and below long-lasting snowdrifts. Common species include *Geum rossii, Polygonum bistortoides,* and *Primula parryi. Caltha leptosepala, Potentilla diversifolia, Sedum rhodanthum,* and *Stellaria longipes* reach their upper elevational limit of 3627 m in this community type on the north-facing slope of Delano Peak.

RIVULET.—Alpine rivulets from melting snowfields are mostly transitory and occur only in the southern (Bullion Canyon Volcanics) portion of the alpine region. *Cardamine cordifolia, Deschampsia cespitosa, Delphinium occidentale* var. *barbeyi,* and *Mertensia arizonica* occur at lower elevations while *Caltha leptosepala, Pedicularis parryi,* and *Salix arctica* occur more commonly at higher elevations. *Polygonum bistortoides* and *Primula parryi* are common throughout this community type. Two rivulets on the flanks of Delano Peak (to about 3444 m in elevation) persist throughout the summer; *Epilobium halleanum, Juncus drummondii, Mimulus tilingii,* and *Saxifraga odontoloma* occur at their upper elevational limit at these continually moist and marginally alpine sites.

GRAVELLY BARREN.—This is perhaps the most distinctive alpine community type in the Tushar Mountains. It occurs on saddles of ridgecrests and on many of the higher tributary drainages between Lake Peak and Mount Belknap where snow accumulations are long lasting; plant cover is only 0 to about 20% on largely unaltered, gravelly, grayish parent material. Some of the relatively few species that occur here are *Calyptridium umbellatum, Elymus scribneri, Ivesia gordonii, Phlox pulvinata, Polemonium viscosum, Senecio amplectens,* and *S. canus.* The endemic *Draba sobolifera* frequently flowers in gravel at the edge of receding snowbanks. Isolated 'hanging' patches of *Geum rossii* turf are sometimes present, indicating possible recent erosion of surrounding material. Gravelly barrens usually intergrade into dry meadow or talus/scree communities over relatively short distances.

BEDROCK.—Plant growth on exposures of bedrock is restricted to rock crevices and ledges where pockets of soil have accumulated. Species present include many of those present on similar aspects in surrounding dry and mesic meadow communities. A unique assemblage of species that occasionally occurs on north-facing exposures includes *Artemisia scopulorum, Carex heteroneura, Cystopteris fragilis, Erigeron compositus, Geum rossii, Oxyria digyna, Saxifraga caespitosa, S. debilis,* and *Stellaria longipes.*

TALUS/SCREE.—Colluvial deposits are most common in the area composed of the Mount Belknap Volcanics and along the glaciated portions of the main ridgecrest. *Arenaria nuttallii, Cerastium beeringianum, Erigeron compositus,* and *Polemonium viscosum* are commonly present on all exposures while *Artemisia scopulorum, Geum rossii,* and *Primula parryi* are more common on more mesic north- and east-facing slopes within this community type.

THE FLORA

The alpine flora of the Tushar Mountains consists of 171 species from 102 genera and 34 families. The largest families are Asteraceae (29 species), Poaceae (20), Brassicaceae (13), Rosaceae (12), Cyperaceae (11), Caryophyllaceae (10), Fabaceae (8), Ranunculaceae (7), and Scrophulariaceae (7). The largest genera are *Carex, Poa,* and *Potentilla* with 11, 8, and 7 species, respectively, while *Saxifraga* and *Senecio* are each represented by five species. *Bromus inermis* and *Taraxacum officinale* are the only introduced species occurring above timberline. The species list is presented near the end of this paper.

Thirteen taxa appear to be restricted to the alpine area: *Astragalus australis* var. *glabriusculus, Carex elynoides, C. haydeniana, C. nardina, Claytonia megarhiza, Hymenoxys grandiflora, Lychnis apetala* var. *kingii, Poa pattersonii, Potentilla concinna, Salix arctica, Saxifraga caespitosa, Townsendia condensata,* and *Valeriana acutiloba.*

Three taxa (1.8% of the alpine flora) are endemic to high elevations in the Tushar Mountains. *Draba sobolifera* and *Senecio castoreus* are most common in gravelly barren and talus/

scree communities above timberline while *Cirsium eatonii* var. *harrisonii* is most common on subalpine talus/scree slopes. Other Utah endemics found in the alpine are *Agoseris glauca* var. *cronquistii*, *Astragalus perianus*, *Castilleja parvula* var. *parvula*, *Gilia tridactyla*, and *Lesquerella wardii*.

The perennial herb life form accounts for 86.4% of the indigenous alpine flora. This figure includes 143 species of angiosperms (110 dicots and 33 monocots), one spikemoss, and two ferns. Ten species of shrubs (5.9% of the flora) are present (two of which are gymnosperms). The remaining 13 indigenous taxa are considered to be annual or biennial to short-lived perennials. Only 1.8% of the flora (*Chenopodium atrovirens*, *Gentianella tenella*, and *Polygonum douglasii*) is classified as strictly annual though Spira (1987) reports *Gentianella tenella* to be strictly biennial in the alpine of the White Mountains, CA. Perennial herbs increase in importance at higher elevations and comprise 94.6% of the species (53 of 56 taxa—with exceptions being *Androsace septentrionalis*, *Draba crassifolia*, and *Salix arctica*) known to occur in the area of 0.6 km^2 above the elevation of 3596 m on Delano Peak. A similar life form composition is reported for the alpine flora of the Teton Range (Spence and Shaw 1981).

Species richness and habitat diversity are greatest in the vicinity of Delano Peak because of this peak's geologic substrate, glacial history, and elevation. Erosion of the Bullion Canyon Volcanics has produced a mostly plateau-like topography conducive to soil formation and associated meadow communities. The northern and eastern slopes of Delano Peak, though glaciated, are relatively gentle as compared to the cliff-like glacial headwalls present along much of the main ridgecrest; persistent snowdrifts (sometimes lasting throughout the summer), which are necessary for the growth of some alpine species (Billings 1978) and which provide moisture to lower elevations, are thus able to form on these less-insolated, high-elevation, leeward slopes. All eight types of plant communities and a minimum of 101 species (59.8% of the indigenous alpine flora) are known to occur within a radius of 1.0 km of the summit within an area of 3.14 km^2 (16.3% of the alpine area).

The northern portion of the alpine region composed of the weathering-resistant Mount Belknap Volcanics is floristically poor despite the presence of the second and third highest peaks; no vascular plants were observed above the elevation of 3536 m on Mount Belknap. A depauperate alpine flora of about 65 species occurs on the ridgecrest cushion plant communities, block slopes, and in the talus/scree and gravelly barren communities and small patches of mesic meadow that occur on the ridges and flanks of these summits; *Cryptogramma crispa* and *Poa pattersonii* apparently occur in the alpine only on this formation, however. Soil formation and plant growth on this substrate may be hindered by unfavorable nutrient availability as occurs locally in hydrothermally altered, highly acidic exposures at the base of the range (Salisbury 1964).

PLANT GEOGRAPHY

The Tushar Mountains are located on the western margin of a floristically similar highland region known as the Southern Rocky Mountains. This area, which includes most of Colorado and parts of adjacent states, contains the greatest concentration of alpine tundra in the United States outside of Alaska (Weber 1965). One hundred fifty-five of the 169 indigenous alpine species of the Tushar Mountains are also reported by Weber and Wittmann (1992) for the flora of Colorado.

Statistical comparison with 14 neighboring alpine floras shows the Tushar alpine flora to be most similar to the adjacent northerly floras of the Wasatch and Uinta ranges of Utah and the Teton Range, Wyoming, with Sorensen's similarity indices of 52.8, 50.2, and 48.8%, respectively (Table 1). The relatively continuous "Teton-Wasatch-High Plateau mainland mountain system" (Harper et al. 1978), which is perhaps best illustrated as an elevated (2000 m and higher elevation) corridor in Figure 19 in Reveal (1979) over which direct migration of alpine species may have occurred during glacial times (Billings 1978) and which has previously been noted to be a migration route for Utah's boreal species (Harper et al. 1978, Welsh 1978, Reveal 1979, and Welsh 1993), has thus likely been a primary source area for development of the alpine flora of the Tushar Mountains. In particular, *Calyptridium umbellatum*, *Cymopterus hendersonii*, *Synthris pinnatifida*, and *Townsendia condensata* appear to have migrated to the Tushars via this north-to-

TABLE 1. Floristic similarity indices between the alpine flora of the Tushar Mountains, UT, and representative neighboring alpine floras. The index of similarity used is that of Sorensen (Mueller-Dombois and Ellenberg 1974). Mainland area floras are part of a relatively continuous mountain system such as the Teton-Wasatch-High Plateau system in contrast to the more isolated mountain floras of the Great Basin and portions of the Colorado Plateau (Harper et al. 1978).

Flora[a]	Number of indigenous alpine species	Alpine-to-alpine distance from Tushar Mts (km)	Percent similarity
MAINLAND AREAS			
1. Wasatch Mountains, UT	202	157	52.8
2. Uinta Mountains, UT	257	269	50.2
3. San Juan Mountains, CO	250	410	44.9
4. Sawatch Range, CO	285	507	45.4
5. Teton Range, WY	216	573	48.8
6. Indian Peaks area, CO	249	596	42.1
7. Pioneer Mountains, ID	130	600	36.8
8. Sangre de Cristo Mountains, NM	157	627	40.5
9. Beartooth Plateau, WY-MT	185	750	36.2
MOUNTAIN ISLANDS			
10. Henry Mountains, UT	47	136	32.4
11. Snake Range, NV	43	171	25.5
12. Deep Creek Mountains, UT	81	198	51.2
13. San Francisco Peaks, AZ	82	332	44.6
14. Ruby Mountains, NV	150	345	42.0

[a] Alpine floras are from the following sources: (1) Arnow et al. (1980) and voucher specimens from Allred (1975) and Collins (1980); (2) Lewis (1970), Goodrich and Neese (1986), and Goodrich (1994); (3) Webber et al. (1976) and Hartman and Rottman (1985); (4) Hartman and Rottman (1988); (5) Spence and Shaw (1981); (6) Komarkova (1979); (7) Moseley and Bernatas (1992); (8) Baker (1983); (9) Johnson and Billings (1962); (10) Neese (1981); (11) Lewis (1973); (12) McMillan (1948); (13) Schaack (1983) and Schaack and Morefield (1985); (14) Loope (1969) and Lewis (1971).

south route, inasmuch as they occur in western Wyoming (Dorn 1988) but are unreported from Colorado (Weber and Wittmann 1992). A total of 158 of the indigenous Tushar alpine species are reported by Dorn (1988) for the flora of Wyoming. The alpine flora of the Tushar Mountains is more similar to that of the Teton Range, Wyoming, than to any of the compared Colorado alpine floras despite a greater distance of up to 160 km (Table 1). Proximity along the same migrational pathway thus appears to be an important factor in floristic similarity.

The apparent effectiveness of the Teton-Wasatch-High Plateau migration route is further illustrated by 13 boreal species occurring in the alpine of the Tushars which are apparently at a southern margin of distribution within the longitudes of Utah: *Astragalus australis, Carex nardina, Lychnis apetala,* and *Salix arctica* are arctic species (Polunin 1959) not known to occur further south in Utah (Albee et al. 1988) or in adjacent Arizona (Lehr 1978). A total of 44 alpine species from the Tushars (26.0% of the indigenous alpine flora) are reported by Polunin (1959) as also occurring in the Arctic. Other alpine species at an apparent southern margin of distribution are *Antennaria alpina* var. *media, Arenaria nuttallii, Calyptridium umbellatum, Chamaerhodos erecta, Claytonia megarhiza, Hymenoxys grandiflora, Poa pattersonii, Saxifraga adscendens,* and *Townsendia condensata.* Nonalpine boreal species at a southern margin of distribution in this range include *Arnica diversifolia, Aster engelmannii, Carex deweyana, C. hoodii, C. luzulina, Draba lanceolata, Hieracium gracile, Leucopoa kingii, Microseris nutans,* and *Mitella pentandra.*

Though migration of high-elevation species has occurred between the Colorado Rockies and the La Sal Mountains of southeastern Utah (Holmgren 1972, Welsh 1993), significant migration of alpine species further west to the Tushar Mountains has perhaps been limited by an area of relatively low elevation termed the "Colorado Plateau migrational barrier" by Hadley (1987). The isolated Henry Mountains, located midway between the Tushar and La Sal ranges (Fig. 1), have a meager alpine flora of 47 species; absent there are common alpine species such as *Geum rossii, Oxyria digyna, Polygonum bistortoides,* and *Silene acaulis* (Neese 1981). These and other alpine species may have been eliminated from the Henry Mountains by the warmer post-glacial hypsithermal climate (Neese 1981), however, thus masking the true effectiveness of the Colorado Plateau as a migrational barrier to high-elevation species.

Species richness, which is strongly correlated with area on mountains (Harper et al. 1978, Hadley 1987), also appears to affect floristic similarity as the Tushar alpine flora generally has higher indices of similarity with the larger and generally more distant mainland floras (Table 1); Harper et al. (1978) note that the isolated mountain floras of the Intermountain West have fewer species per unit area than adjacent mainlands and also an uneven stocking of species as a result of greater randomness of colonization and/or extinction. The isolated alpine floras of the east central Great Basin to the west of the Tushars (Loope 1969), the San Francisco Peaks to the south (Moore 1965), and the Henry Mountains to the east (Neese 1981) are slightly to extremely depauperate examples of the Rocky Mountains alpine flora.

The Tushar alpine flora is also slightly depauperate in comparison with most other neighboring mainland area floras (Table 1); this is likely due to the limited alpine area (in comparison, the Uinta Mountains have an alpine area of about 1000 km^2 [Lewis 1970]), scarcity of wet meadows and rivulets, and presence of the talus-forming Mount Belknap Formation. The smaller Tushar alpine flora may be a factor in the relatively low maximum similarity index of 52.8% with the Wasatch Mountains; Hartmann and Rottman (1988) report a similarity index range of 72.5–73.3% between the larger alpine floras in Colorado.

The alpine flora and vegetation of the Tushar Mountains are remarkably diverse given the relatively small alpine area. Interesting, too, are the number of endemic taxa and species that reach a southern limit of distribution here. The wide-ranging alpine species *Claytonia megarhiza*, *Poa pattersonii*, and *Saxifraga adscendens* are disjunct here with other in-state distributions only in the Uinta and La Sal ranges, while *Townsendia condensata* occurs nowhere else in the state (Albee et al. 1988, Welsh et al. 1993).

Alpine environments are in general fragile and easily susceptible to disturbance (Billings 1973). This fragility is locally compounded by poor soil-forming characteristics of some igneous members and by the questionable introduction of Rocky Mountain goats to the range in 1986. There is evidence these animals feed on the endemic *Castilleja parvula*, and they endanger the species diversity of the alpine area by grazing at scarce alpine wet sites.

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ANNOTATED LIST OF VASCULAR PLANTS

The following list of families, genera, and species is arranged alphabetically within the divisions of Cronquist et al. (1972). Community type(s) and maximum elevation noted for each taxon are based on field notes and herbarium specimen label information. The following abbreviations are used for community types: cushion plant (CP), dry meadow (DM), mesic meadow (MM), wet meadow (WM), rivulet (RI), gravelly barren (GB), bedrock (BR), and talus/scree (TS). Frequency of occurrence for most taxa is estimated using the following scale from Thorne (1967): rare, 1–3 collections or observation stations; infrequent, 4–7 stations; frequent, 8–12 stations; common, 13+ stations. Life form is listed as a = annual, ab = annual or biennial, ap = annual to short-lived perennial, bp = biennial to perennial, p = perennial herb, and s = shrub. Species that also occur in the Arctic (Polunin 1959) are followed by an asterisk (*).

I collected *Botrychium lunaria*, *Juncus mertensianus*, *Pedicularis groenlandica*, and *Salix planifolia* at a seep below local timberline at an elevation of 3389 m, and *Draba lanceolata* has been collected at timberline (Welsh et al. 14015). These and other taxa may eventually be discovered from the alpine area. *Erigeron humilis* and *Taraxacum ceratophorum* have recently been reported for the Tushars (Cronquist 1994), but I have seen no specimens.

DIVISION LYCOPODIOPHYTA

Selaginellaceae

***Selaginella watsonii* Underw.**; rock crevices in CP, DM, MM, BR, and TS to 3658 m; common; p.

DIVISION POLYPODIOPHYTA

Polypodiaceae

***Cryptogramma crispa* (L.) R. Br. var. *acrostichoides* (R. Br.) C. B. Clarke**; TS to 3304 m; rare; p.

***Cystopteris fragilis* (L.) Bernh.**; rock crevices in DM, MM, RI, BR, and TS to 3505 m; frequent; p.*

DIVISION PINOPHYTA

Cupressaceae

***Juniperus communis* L. var. *depressa* Pursh**; DM at 3444 m in shelter of boulder on south-facing slope; rare; s.*

Pinaceae

***Picea engelmannii* Parry**; DM, MM, and TS to 3566 m; common; s.

DIVISION MAGNOLIOPHYTA

CLASS MAGNOLIOPSIDA

Apiaceae

***Cymopterus hendersonii* (Coult. & Rose) Cronq.**; CP, BR, and TS to 3627 m; frequent; p.

***Cymopterus lemmonii* (Coult. & Rose) Dorn [*Pseudocymopterus montanus* (Gray) Coult. & Rose]**; CP, DM, MM, RI, and TS to 3700 m; common; p.

Asteraceae

***Achillea millefolium* L. ssp. *lanulosa* (Nutt.) Piper**; DM, MM, and RI to 3548 m; common; p.*

***Agoseris aurantiaca* (Hook.) Greene var. *purpurea* (Gray) Cronq.**; MM(?) to ca 3505 m; rare; p.

***Agoseris glauca* (Pursh) Raf. var. *cronquistii* Welsh**; DM to 3353 m; infrequent; p.

***Agoseris glauca* (Pursh) Raf. var. *dasycephala* (T. & G.) Jepson**; CP to 3414 m; rare; p.

***Antennaria alpina* (L.) Gaertner var. *media* (Greene) Jepson [*A. media* Greene]**; CP, MM, and BR to 3487 m; common; p.

***Antennaria microphylla* Rydb.**; DM to 3536 m; rare; p.

***Arnica mollis* Hook.**; BR/MM to 3444 m; rare; p.

***Artemisia frigida* Willd.**; CP and DM to 3505 m; rare; s.*

***Artemisia ludoviciana* Willd. var. *incompta* (Nutt.) Cronq.**; CP, DM, MM, and RI to 3475 m; common; p.

***Artemisia scopulorum* Gray**; MM, WM, RI, BR, and TS to 3703 m; common; p.

***Cirsium eatonii* (Gray) Robins. var. *harrisonii* Welsh**; TS to 3444 m; rare; p.

***Crepis nana* Richards.**; CP, GB, and TS to 3475 m; frequent; p.*

***Erigeron compositus* Pursh var. *glabratus* Macoun**; CP, DM, GB, BR, and TS to 3706 m; common; p.*

***Erigeron simplex* Greene**; MM to 3700 m; frequent; p.

***Erigeron speciosus* (Lindl.) DC. var. *uintahensis* (Cronq.) Welsh [*E. uintahensis* Cronq.]**; DM to 3414 m; rare; p.

***Erigeron ursinus* D. C. Eaton**; CP, MM, and RI to 3536 m; common; p.

***Haplopappus clementis* (Rydb.) Blake**; MM and GB to 3578 m; common; p.

***Haplopappus macronema* Gray**; CP, DM, GB, and TS to 3536 m; common; s.

***Helenium hoopesii* Gray [*Dugaldia hoopesii* (Gray) Rydb.]**; DM and MM to 3566 m; common; p.

***Hymenopappus filifolius* Hook. var. *nudipes* (Maguire) Turner**; DM and GB to 3561 m; infrequent; p.

***Hymenoxys grandiflora* (T. & G.) Parker**; "grassy tundra above timberline" at 3505 m; rare; p. The only record from the range is K. F. Parker et al. 6354 at the Rancho Santa Ana Botanic Garden.

***Senecio amplectens* Gray var. *holmii* (Greene) Harrington**; MM, GB, and BR to 3700 m; common; p.

***Senecio canus* Hook.**; DM and GB to 3609 m; common; p.

***Senecio castoreus* Welsh**; CP, GB, and TS to 3536 m; infrequent; p.

***Senecio eremophilus* Richards. var. *kingii* (Rydb.) Greenman**; DM and MM to 3536 m; infrequent; p.

***Senecio werneriaefolius* (Gray) Gray**; TS to 3505 m; frequent; p.

***Solidago multiradiata* Ait.**; DM, MM, GB, and BR to 3700 m; common; p.*

***Solidago parryi* (Gray) Greene [*Haplopappus parryi* Gray]**; MM to 3505 m; infrequent; p.

***Taraxacum officinale* Weber**; DM and TS to 3536 m; infrequent; introduced p.

***Townsendia condensata* D. C. Eaton**; CP and GB at 3505–3609 m; infrequent; p.

Boraginaceae

***Mertensia arizonica* Greene**; DM, MM, and RI to 3505 m; common; p.

Brassicaceae

***Arabis drummondii* Gray**; DM to 3414 m; infrequent; bp.

***Arabis lemmonii* Wats.**; MM and BR to 3402 m; rare; p.

***Cardamine cordifolia* Gray**; RI to 3444 m; infrequent (locally common); p.

Descurainia richardsonii **(Sweet) Schulz var. *brevipes* (Nutt.) Welsh & Reveal**; RI and TS to 3475 m; infrequent; ab.

Draba aurea **Vahl**; MM and BR to 3688 m; rare; p.*

Draba crassifolia **Graham**; MM and RI to 3700 m; frequent; ap.*

Draba sobolifera **Rydb.**; MM, GB, BR, and TS to 3688 m; common; p.

Draba stenoloba **Ledeb.**; MM to 3505 m; rare; ap.*

Erysimum asperum **(Nutt.) DC.**; DM to 3441 m; rare; bp.

Lesquerella wardii **Wats.**; DM and GB to 3609 m; frequent; p.

Physaria chambersii **Rollins var. *chambersii***; GB to 3414 m; rare; p.

Smelowskia calycina **C. A. Mey. var. *americana* (Regel & Herder) Drury & Rollins**; CP, DM, MM, BR, and TS to 3703 m; common; p.*

Thlaspi montanum **L. var. *montanum***; CP, MM, and TS to 3475 m; common; p.

Caprifoliaceae

Sambucus racemosa **L. var. *microbotrys* (Rydb.) Kearney & Peebles**; DM and TS to 3444 m; infrequent; s.

Caryophyllaceae

Arenaria nuttallii **Pax**; CP, MM, GB, and TS to 3505 m; common; p.

Arenaria obtusiloba **(Rydb.) Fern.**; MM and WM to 3676 m; common; p.*

Arenaria rubella **(Wahl.) J. E. Sm.**; CP, DM, MM, and RI to 3688 m; frequent; p.*

Cerastium beeringianum **C. & S.**; CP, DM, MM, WM, BR, and TS to 3700 m; common; p.*

Lychnis apetala **L. var. *kingii* (Wats.) Welsh [*L. kingii* Wats.]**; CP, DM, and MM at 3536–3688 m; frequent; p.*

Lychnis drummondii **(Hook.) Wats.**; DM, MM, and BR to 3487 m; frequent; p.

Sagina saginoides **(L.) Britt.**; MM and RI to 3414 m; rare; bp.*

Silene acaulis **L. var. *subacaulescens* (F. Williams) Fern. & St. John**; CP, MM, WM, BR, and TS to 3676 m; common; p.*

Stellaria longipes **Goldie**; DM, MM, WM, BR, and TS to 3627 m; common; p.*

Stellaria umbellata **Turcz.**; MM, RI, and TS to 3615 m; frequent; p.

Chenopodiaceae

Chenopodium atrovirens **Rydb.**; DM in disturbed soil (pocket gophers?) at 3548 m; rare; a.

Crassulaceae

Sedum rhodanthum **Gray**; MM and WM to 3627 m; infrequent; p.

Fabaceae

Astragalus australis **Fisch. var. *glabriusculus* (Hook.) Isely [*A. aboriginum* Richards.]**; CP and GB at 3505–3609 m; infrequent; p.*

Astragalus miser **Dougl. var. *oblongifolius* (Rydb.) Cronq.**; DM, MM, and GB to 3706 m; common; p.

Astragalus perianus **Barneby**; DM and GB to 3566 m; infrequent; p.

Lupinus argenteus **Pursh var. *rubricaulis* (Greene) Welsh**; DM to 3463 m; rare; p.

Lupinus lepidus **Dougl. var. *utahensis* (Wats.) C. L. Hitchc. [*L. caespitosus* Nutt. var. *utahensis* (Wats.) B. Cox]**; DM, MM, and GB to 3572 m; frequent; p.

Oxytropis oreophila **Gray var. *oreophila***; CP, DM, MM, and GB to 3706 m; common; p.

Oxytropis parryi **Gray**; DM and MM to 3633 m; infrequent; p.

Trifolium longipes **Nutt. var. *rusbyi* (Greene) Harrington**; MM to 3597 m; frequent; p.

Gentianaceae

Gentiana parryi **Engelm.**; DM to 3389 m; rare; p.

Gentianella amarella **(L.) Borner**; DM and MM to 3535 m; frequent; ab.*

Gentianella tenella **(Rottb.) Borner**; MM and WM to 3566 m; rare; a (b?).*

Swertia radiata **(Kellogg) Kuntze [*Frasera speciosa* Dougl.]**; MM and TS to 3475 m; rare; p.

Grossulariaceae

Ribes cereum **Dougl.**; DM and BR to 3536 m; frequent; s.

Ribes inerme **Rydb.**; DM (among rocks) and TS to 3438 m; rare; s.

Ribes montigenum **McClatchie**; DM, MM, RI, and TS to 3627 m; common; s.

Hydrophyllaceae

Phacelia hastata **Dougl.**; DM in gravelly soil to 3444 m; rare; p.

Phacelia sericea **(Graham) Gray var. *ciliosa* Rydb.**; DM to 3475 m; rare; p.

Lamiaceae

Monardella odoratissima **Benth.**; TS to 3475 m; rare; p.

Linaceae

Linum perenne **L. ssp. *lewisii* (Pursh) Hulten**; MM in gravelly soil at 3536 m; rare; p.*

Onagraceae

Epilobium angustifolium **L.**; TS to 3414 m; rare; p.*

Epilobium halleanum **Hausskn.**; RI to 3444 m; rare (locally common); p.

Epilobium saximontanum **Hausskn.**; RI to 3487 m; rare (locally common); p.

Polemoniaceae

Gilia tridactyla **Rydb.**; CP and TS to 3414 m; rare; p.

Phlox pulvinata **(Wherry) Cronq.**; CP, DM, MM, GB, BR, and TS to 3706 m; common; p.

Polemonium pulcherrimum **Hook. var. *delicatum* (Rydb.) Cronq.**; DM and MM to 3444 m; infrequent; p.*

Polemonium viscosum **Nutt.**; DM, MM, GB, BR, and TS to 3633 m; common; p.

Polygonaceae

Eriogonum umbellatum **Torr. var. *porteri* (Small) Stokes**; DM, MM, and BR to 3566 m; frequent; p.

Oxyria digyna **(L.) Hill**; MM, GB, BR, and TS to 3658 m; common; p.*

Polygonum bistortoides Pursh; MM, WM, and RI to 3676 m; common; p.

Polygonum douglasii Greene var. _douglasii_; DM to 3444 m; rare; a.

Rumex salicifolius Weinm. ssp. _triangulivalvis_ Danser; DM, MM, RI, and BR to 3499 m; frequent; p.

Portulacaceae

Calyptridium umbellatum (Torr.) Greene var. _caudicifera_ Gray; MM and GB to 3536 m; infrequent; ap.

Claytonia megarhiza (Gray) Parry; BR and TS at 3475 to 3615 m; rare; p.

Lewisia pygmaea (Gray) Robins.; MM and RI to 3597 m; frequent; p.

Primulaceae

Androsace septentrionalis L.; DM, MM, RI, and TS to 3700 m; common; ab.*

Primula parryi Gray; MM, WM, RI, BR, and TS to 3658 m; common; p.

Ranunculaceae

Anemone multifida Poir.; CP and MM to 3487 m; rare; p.

Aquilegia scopulorum Tidestr.; TS to 3438 m; infrequent; p. As noted in Welsh et al. (1993), some specimens are completely transitional with *A. caerulea* James.

Caltha leptosepala DC. var. _leptosepala_; MM, WM, and RI to 3627 m; frequent; p.

Delphinium occidentale (Wats.) Wats. var. _barbeyi_ (Huth) Welsh [_D. barbeyi_ (Huth) Huth]; DM, RI, and TS to 3475 m; common; p.

Ranunculus eschscholtzii Schlect.; TS to ca 3490 m; rare; p.

Ranunculus inamoenus Greene; DM and RI to 3597 m; common; p.

Thalictrum fendleri Engelm.; DM (in shelter of *Ribes montigenum*) to 3414 m; rare; p.

Rosaceae

Chamaerhodos erecta Bunge var. _parviflora_ (Nutt.) C. L. Hitchc.; CP and DM to 3505 m; rare; bp.

Geum rossii (R. Br.) Ser. var. _turbinatum_ (Rydb.) C. L. Hitchc.; CP, DM, MM, WM, RI, GB, TS, and BR to 3700 m; common; p.*

Ivesia gordonii (Hook.) T. & G.; DM and GB to 3609 m; infrequent; p.

Potentilla concinna Richards. var. _proxima_ (Rydb.) Welsh & Johnston; DM and TS at 3353 to 3536 m; infrequent; p.

Potentilla diversifolia Lehm. var. _diversifolia_; WM, RI, and TS to 3627 m; frequent; p.

Potentilla glandulosa Lindl. var. _intermedia_ (Rydb.) C. L. Hitchc.; DM, MM, and TS to 3487 m; common; p.

Potentilla gracilis Dougl. var. _pulcherrima_ (Lehm.) Fern.; DM to 3463 m; frequent; p.

Potentilla hippiana Lehm.; DM to 3414 m; p.

Potentilla ovina Macoun var. _decurrens_ (Wats.) Welsh & Johnston; CP and DM to 3475 m; infrequent; p.

Potentilla pensylvanica L. var. _pensylvanica_; CP, DM, MM, and TS to 3700 m; common; p.*

Rubus idaeus L. ssp. _melanolasius_ (Dieck) Focke.; TS to 3414 m; rare; s.

Sibbaldia procumbens L.; MM, RI, and BR to 3627 m; common; p.*

Salicaceae

Salix arctica Pallas var. _petraea_ Anderss.; MM, WM, and RI at 3444 to 3676 m; frequent (locally common); s.*

Saxifragaceae

Heuchera rubescens Torr. var. _rubescens_; BR to 3444 m; rare; p.

Saxifraga adscendens L. var. _oregonensis_ (Raf.) Breitung; MM (among rocks) to 3676 m; rare; p.

Saxifraga caespitosa L. var. _minima_ Blake; MM, WM, and BR at 3566 to 3676 m; infrequent; p.*

Saxifraga debilis Engelm.; MM and BR to 3658 m; common; p.

Saxifraga odontoloma Piper; RI to 3444 m; rare; p.

Saxifraga rhomboidea Greene; DM, MM, WM, and RI to 3700 m; common; p.

Scrophulariaceae

Castilleja miniata Dougl.; DM to 3535 m; infrequent; p.

Castilleja parvula Rydb. var. _parvula_; DM and MM to 3688 m; common; p.

Mimulus tilingii Regel; RI to 3414 m; rare; p.

Pedicularis parryi Gray var. _parryi_; MM, WM, and RI to 3627 m; common; p.

Penstemon whippleanus Gray; MM and BR to 3450 m; frequent; p.

Synthris pinnatifida Wats. var. _laciniata_ Gray; DM, MM, WM, RI, and BR to 3627 m; common; p.

Veronica wormskjoldii R. & S.; MM and RI to 3487 m; rare; p.*

Valerianaceae

Valeriana acutiloba Rydb.; DM and MM at 3414 to 3567 m; infrequent; p.

Valeriana edulis Nutt.; CP, DM, and MM to 3599 m; infrequent; p.

Valeriana occidentalis Heller; DM to 3353 m; rare; p.

Violaceae

Viola canadensis L.; BR and TS to 3444 m; rare; p.

Viola nuttallii Pursh; DM to 3414 m; rare; p.

CLASS LILIOPSIDA

Cyperaceae

Carex albonigra Mack.; CP and MM to ca 3658 m; infrequent; p.

Carex ebenea Rydb.; RI to 3444 m; rare; p.

Carex egglestonii Mack.; DM to 3414 m; rare; p.

Carex elynoides H. T. Holm; CP, DM, MM, and TS at 3353 to 3706 m; common; p.

Carex haydeniana Olney; MM, RI, GB, and BR at 3414 to 3566 m; common; p.

Carex heteroneura W. Boott var. _chalciolepis_ (H. T. Holm) F. Hermann; the intergrading var. *epapillosa* F. Hermann also occurs in the range though perhaps not in the alpine; MM and BR to ca 3658 m; common; p.

Carex microptera Mack.; DM (?) to 3414 m; rare; p.

Carex nardina Fries; MM at 3505 m; rare; p.*

Carex nova Bailey; unknown community at ca 3505 m; rare; p.

Carex phaeocephala Piper; CP, DM, MM, and GB to 3566 m; common; p.

Carex rossii F. Boott; DM (?) to ca 3353 m; rare; p.

Juncaceae

Juncus drummondii **E. Mey.**; RI to 3444 m; rare; p.

Luzula spicata **(L.) DC.**; MM, WM, and BR to 3627 m; common; p.*

Liliaceae

Zigadenus elegans **Pursh**; MM, WM, and RI to 3536 m; infrequent; p.*

Poaceae

Agrostis variabilis **Rydb.**; MM to 3383 m; rare; p.

Bromus ciliatus **L.**; MM to 3414 m; rare; p.

Bromus inermis **Leysser**; roadside adjacent to MM at 3487 m; rare; introduced p.

Calamagrostis purpurascens **R. Br.**; TS to 3414 m; rare; p.*

Deschampsia cespitosa **(L.) Beauv.**; MM and RI to 3499 m; infrequent; p.*

Elymus elymoides **(Raf.) Swezey [*Sitanion hystrix* (Nutt.) J. G. Sm.]**; DM to ca 3505 m; rare; p.

Elymus scribneri **(Vasey) Jones [*Agropyron scribneri* Vasey]**; DM, GB, and TS to 3578 m; common; p.

Elymus trachycaulus **(Link) Gould [*Agropyron trachycaulum* (Link) Malte]**; DM and MM to 3566 m; common; p.*

Festuca ovina **L. var. *brevifolia* (R. Br.) Wats.**; CP, DM, MM, GB, BR, and TS to 3706 m; common; p.*

Phleum alpinum **L.**; MM and RI to 3487 m; frequent; p.*

Poa arctica **R. Br.**; CP, MM, WM, BR, and TS to 3700 m; frequent; p.*

Poa fendleriana **(Steudel) Vasey**; DM to 3383 m; frequent; p.

Poa glauca **Vahl [*P. glauca* ssp. *rupicola* (Nash) W. A. Weber; *P. interior* Rydb.]**; CP, DM, MM, GB, and TS to 3536 m; common; p.*

Poa nervosa **(Hook.) Vasey**; TS to 3414 m; infrequent; p.

Poa pattersonii **Vasey**; TS at 3505 m; rare; p.

Poa pratensis **L.**; MM to 3444 m; rare?; possibly introduced p.*

Poa reflexa **Vasey & Scribn.**; MM and RI to 3536 m; common; p.

Poa secunda **Presl [*P. sandbergii* Vasey]**; CP, DM, and TS to 3475 m; frequent; p.

Stipa lettermanii **Vasey**; DM and MM to 3475 m; frequent; p.

Trisetum spicatum **(L.) Richter**; CP, MM, BR, and TS to 3700 m; common; p.*

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ECOLOGY OF *CELTIS RETICULATA* IN IDAHO

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ABSTRACT.—The small deciduous tree *Celtis reticulata* (netleaf hackberry) reaches its northern limit in Idaho, where, contrary to most of its western range, it often occurs as an overstory dominant. Two hundred fifty stands of this tree were sampled throughout Idaho. *Celtis* is slow-growing, averaging 4 m tall at 50 yr, and long-lived (to 300–400 yr). It occurs in a variety of habitats, from riparian to rocky uplands. Trees grow best where topographically sheltered, such as in draws and narrow canyons, and where soils are loamy. Although plants grow more slowly as surface rock cover increases, stands are often associated with rock, with a mean surface cover of 39% rock. Differences in growth rates were unrelated to parent material and aspect. Most stands are reproducing, in spite of habitat degradation caused by overgrazing, alien plant invasion, and increasing fire frequencies. Stands are typically represented by one dominant cohort; however, young, even-aged stands are rare and are generally found along waterways on stream terraces or at the high-water line. Although slow-growing, *C. reticulata* shows promise for land managers interested in site enhancement. This native species is long-lived, produces fruit used by wildlife, and provides structural diversity in a semiarid landscape (with a maximum height of 12 m) in areas that are becoming increasingly dominated by exotic plant species.

Key words: Celtis reticulata, *netleaf hackberry, ecology, Idaho, growth, longevity, stand structure, recruitment, site characteristics, livestock grazing, rehabilitation.*

Celtis reticulata Torr. (netleaf hackberry, western hackberry) is a deciduous shrub to small tree in the elm family (Ulmaceae), widely distributed in semiarid regions of the western United States (Fig. 1). It occurs in a diversity of habitats, including deciduous riparian woodlands, mountain shrub, wash scrub, and live oak–mixed shrub communities, in rocky canyons, and as scattered individuals in semidesert grasslands, pinyon-juniper and Joshua tree woodlands (Glinski 1977, Plummer 1977, Brown 1982, Albee et al. 1988). Its elevational range is from 200 to 2000 m (Elias 1980). Populations are often small or highly localized (Daubenmire 1970, Dooley and Collins 1984), particularly at the northerly latitudes in the states of Oregon, Washington, and Idaho (Eliot 1938). Despite its broad distribution, little is known about the plant's ecology, presumably due to its position as a minor component in many of its habitats, and its fragmented occurrence (Peattie 1953, Lanner 1983).

While *C. reticulata* is sparsely distributed in Idaho, near its northern limit (Fig. 2), it appears to exhibit wide ecological tolerances. However, it tends toward the warmest portions of canyons, especially southerly aspects (Tisdale 1986). It is a member of both riparian and upland communities in Idaho, where it can occur as a locally abundant, overstory dominant (Huschle 1975, Johnson and Simon 1987). Along the Wiley Reach of the middle Snake River, it forms narrow, but extensive, gallery forests of nearly monospecific stands (Bowler 1981). On steep shoreline escarpments of the lower reaches of the Snake River, in the "Douglas" hackberry vegetation type described by Huschle (1975), it forms a dense, nearly closed canopy. On the gentle shoreline slopes, alluvial fans, and colluvial cones of the lower Snake River, it grows in an open savanna (Daubenmire 1970, Huschle 1975). "Open savanna" is perhaps the best way to describe the appearance of a typical *Celtis* community on an upland site in Idaho, where individuals occur in a random or clumped pattern with extensive areas of grassland between.

Plants produce a small, fleshy drupe in the fall, favored by a variety of birds and mammals (Hayward 1948, Lanner 1983, C. A. Johnson 1990, personal communication). With as many as 41 species of birds associated with *Celtis* communities in Idaho, the tree's importance for wildlife cannot be overemphasized (Asherin and Claar 1976). It provides cover for a variety of big game species, including mule deer and bighorn sheep (Asherin and Claar 1976), as well as much-sought-after shade for domestic

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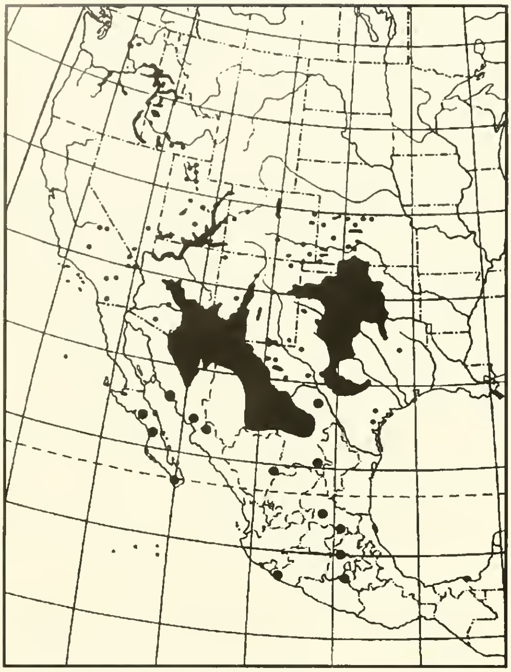

Fig. 1. Global distribution of *Celtis reticulata* (revised from Little 1976).

livestock along the Snake River (Daubenmire 1970).

Due to an apparent tolerance of harsh, water-stressed growing conditions, a strong potential to resprout following disturbances such as fire and herbivory, and its high wildlife values, public land managers are interested in using *C. reticulata* to rehabilitate disturbed habitats. However, we must know more of the growth rate, longevity, stand structure, and ecological tolerances of the species to properly evaluate its potential in site enhancement or rehabilitation projects.

This study sought to answer the following questions: (1) What are the growth rates and longevities of *C. reticulata*, and do they differ with aspect, parent material, soil texture, percent surface rock cover, topographic position, topographic shelter, and grazing intensity of a stand? (2) How does the size class structure of *C. reticulata* stands differ with the environmental parameters listed above? Is the species reproducing in Idaho, and does recruitment differ under different environmental conditions? (3) Are environmental conditions related to differences in growth form of the plant (i.e., the formation of single vs. multiple stems)?

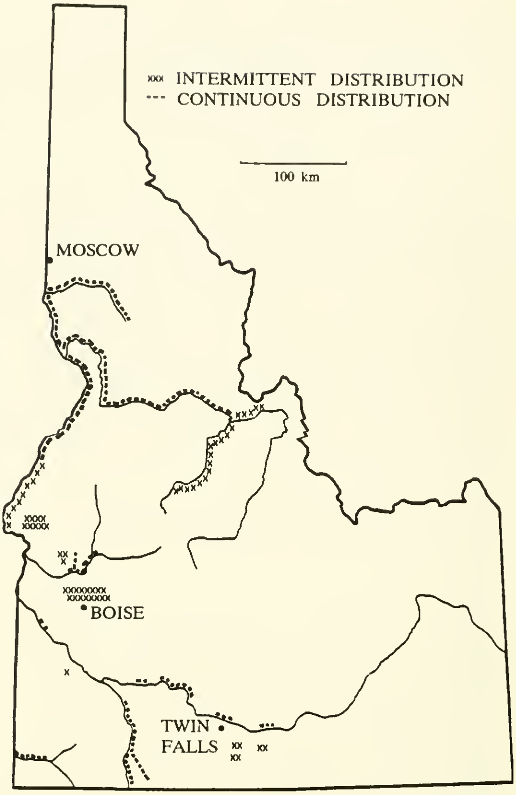

Fig. 2. Idaho distribution of *Celtis reticulata*.

METHODS

Field Methods

Two hundred thirty stands spread over much of the Idaho range of *C. reticulata* were sampled in 1990 and 1991. Approximately 20 stands on the west side of the Snake River, in adjacent Oregon and Washington, were also sampled (total $N = 250$). Stands were selected based on within-site homogeneity of apparent history, topography, and parent material, and a minimum population size of six individuals (many more individuals were usually present). With these constraints for homogeneity, the sampling areas were typically irregularly shaped and small, usually less than 0.25 ha. Stands were chosen to represent a range of sites and disturbance histories.

Stands were assigned to topographic positions (Table 1) that included river terrace, high-water line, draw, rocky draw, bench, toe slope, lower slope, broken lower slope, mid-slope, upper slope, and talus. The 11 categories were narrowly defined on the assumption that

Table 1. Definitions of topographic positions in which *Celtis reticulata* was sampled.

River terrace	Relatively flat horizontal surface cut or built by river or stream action
High-water line	Transition line between flood-tolerant and -intolerant plant species
Draw	Shallow incision in a slope, with <30% total surface rock cover
Rocky draw	Shallow incision in a slope, with >30% total surface rock cover
Bench	Nearly level surface usually well above active floodplains and terraces
Toe slope	Gently inclined, basal part of a slope continuum that grades to the valley, usually <14° slope
Lower slope	Lower 1/3 of a hillside (above the toe slope, when present); if steep (>14°) and toe slope absent, the basal part of the slope that meets the valley floor
Broken lower slope	Similar to lower slope but with extensive surface cover of large boulders and outcrops
Mid-slope	Middle 1/3 of a hillside, relative to the surrounding landscape
Upper slope	Upper 1/3 of a hillside, relative to the surrounding landscape
Talus slope	Coarse, angular rock fragments derived from and lying at the base of cliffs or rock slopes; slopes typically >25°

combining them at a later time, if needed, would be possible. Based on field observation and reconnaissance, the number of stands sampled within each topographic position was approximately proportionate to how frequently those topographic positions were occupied by the species. Stand-level data recorded, in addition to topographic position, included elevation; latitude; longitude; aspect; slope; percent surface rock cover; surface soil texture; parent material; topographic shelter, grazing intensity, total stand density; density within four structural classes, including seedling, juvenile, mature, and decadent individuals; number of cohort modes; and associated dominant plant species (explained below).

Surface soil textures were evaluated by moistening in the field according to the Soil Conservation Service "Guide for Textural Classificaton" (Brady 1974). When soils were unreachable due to surface rock, the surface rock matrix was classified instead. For example, stands on talus slopes had soils categorized as "talus."

Six categories of parent material were identified initially, including granite, sandstone, basalt, river alluvium, rhyolite, and oolitic limestone. However, because of the small sample size of rhyolite (4) and its chemical similarity to granite, the two were combined for analysis. A similar situation existed for oolitic limestone, an uncommon and geographically restricted coarse-grained rock that typically occurred as a lens within sandstone-dominated strata. Therefore, the eight stands on oolitic limestone were combined with sandstone for analysis.

Each stand was categorized by "topographic shelter": open (0), intermediate (1), and sheltered (2). For example, exposed stands growing within a valley were classified as "intermediate," while stands growing in a side canyon of the same valley were classified as "sheltered." "Open" stands were those with unobstructed exposure to solar radiation. They were typically not associated with a major, incised drainage; rather, they faced broad, expansive valleys.

To evaluate recruitment and growth of *C. reticulata* under different livestock grazing pressures, we scored grazing intensity within a stand as none to moderate (1) or extreme (2). Stands scored as extreme were recognized by (1) heavy browsing of trees, with a hedged or "pasture-tree" growth form; (2) elimination of vegetation under trees by trampling; (3) tree roots exposed by soil compaction and erosion; and (4) dominance of alien plant species. Thirty-six of the 250 stands were classified as extreme.

The overall density of *Celtis* stands was categorized as (1) widely scattered [mature individuals more than 10 crown widths apart]; (2) scattered [mature individuals separated by gaps of 4–10 individual crown widths]; (3) subcontinuous [breaks in the total canopy exist but mature individuals average no more than 3 crown widths apart]; or (4) continuous [little open space in the canopy; crowns form a continuous matrix with occasional gaps]. Intermediate sites were recognized with a midpoint value (e.g., 3.5 for stands approaching a closed canopy).

To evaluate the composition of *C. reticulata* stands, densities in four structural classes were also estimated in a similar fashion. The four structural classes were defined as follows: (1) seedling [individual of the year and ≤ 2 yr old]; (2) juvenile [individual >2 yr old and ≤ 1.5 m tall]; (3) mature [>1.5 m tall]; and (4) decadent [>1.5 m tall and experiencing significant dieback, i.e., at least one major dead branch present].

Within each stand at least three individuals, chosen to represent the modal size in the stand, were measured and aged. Modal size was defined as typical size of individuals in the dominant (most abundant) cohort. Measurements recorded for each tree included height, age, diameter at core height (typically 20 cm above ground level), number of live and dead stems, and percent rock cover below the canopy as centered over the main trunk. When two or three modal sizes were present, all modes were sampled for a minimum total of either six or nine individuals. When stands were all-aged with no apparent modal tree size, at least six individuals of the dominant canopy cohort were sampled. The number of modes present, from 1 to 4, with 4 equivalent to an all-aged stand, was recorded as a stand-level variable. Most height measurements were obtained with an 8-m, extendable level rod. For taller trees, height was determined with a clinometer.

Increment cores were taken at the same height the diameter was measured (20 cm). Cores were transported in plastic straws, glued onto slotted boards, sanded, and annual growth rings were counted under a dissecting microscope. When cores did not reach the tree's center (i.e., because of rot), the number of missing years was extrapolated by first subtracting the length of the core from the tree's radius. This remainder was multiplied by the number of rings counted in the core's inner centimeter, which was then added to the number of rings counted for an estimate of the total age. When cores were off-center, the missing radius was estimated by overlaying a clear transparency with a series of circles of known radii over the core, matching the ring pattern in the core with a circle, and multiplying its radius by the number of rings in the centimeter nearest the core's center. This amount was added to the number of counted years to estimate tree age. Small-diameter noncoreable individuals were cut down and a cross section was removed, sanded, and the rings counted as above.

Analytical Methods

Stands were not included in the analysis if the sample size within a particular topographic position or parent material was too small, or if the majority of cores from a stand were illegible after sanding due to contortions in the radial growth. Nine stands were dropped, for a final sample size of 241. SPSS (1988) was used for all analyses.

A heat load index was generated to account for differences in heat load from northeast- to southwest-facing slopes (Whittaker 1960, Muir and Lotan 1985). For each stand, index values were calculated with the following equation, where Θ = aspect in radians east of north: heat load = $(1 - \cos(\Theta - \pi/4))/2$. Index values ranged from 0 (NE slopes) to 1 (SW slopes).

To compare *C. reticulata* growth rate and stand structure differences under various environmental conditions, we developed 50-yr site indices as measures of growth potential (i.e., site quality), as outlined in Husch et al. (1972). Site index is based on average heights of dominant trees at a specified index age (usually 50 or 100 yr) and is the most widely used method of evaluating site quality for tree growth (Husch et al. 1972, Daubenmire 1976). Site index curves are constructed to allow for estimation of site index for stands older or younger than the index age, as index age stands are seldom encountered (Husch et al. 1972).

The commonly used relationship of tree height to age formed the basis for one index, and the relationship of tree diameter to age formed the basis for the second (DeBolt 1992). The best linear fit was achieved when log (height, m) and log (diameter, cm) were regressed on the log of tree age ($R^2 = .25$, $R^2 = .54$, respectively; $N = 939$). The resulting equations were log (height) = 0.428 × log (age) – 0.135 and log (diameter) = 0.764 × log (age) – 0.165. Using these two equations, we obtained the expected (mean) height and diameter at 50 yr, then back-transformed to improve interpretability, yielding an expected size at 50 yr of 3.9 m tall and 13.6 cm in diameter.

For each tree in the data set, the site index was calculated by first finding its residual from the regression line, then shifting this residual to the 50-yr point on the line, which yields an estimated height and diameter at 50 yr. Thus, the equations to calculate site index (SI) for each tree were:

$$\text{Log (height SI)} = 0.591 + (\text{LOGheight} - ((0.428 \times \text{LOGage}) - 0.135))$$

$$\text{Log (diameter SI)} = 1.134 + (\text{LOGdiam} - ((0.764 \times \text{LOGage}) - 0.165))$$

To analyze structural class differences under differing environmental conditions, the variable TYPE, representing types of stand structure, was created. Based on the density of juvenile, mature, and decadent size classes in a stand, the five TYPEs were defined as follows: (1) young (juvenile); (2) mature, nonreproducing, nondecadent; (3) mature, reproducing, nondecadent; (4) mature, reproducing, decadent; and (5) mature, nonreproducing, decadent (Table 2).

Based on field observations, mortality of *C. reticulata* seedlings during year one is extremely high. Because most seedlings were yearlings, seedlings were not used to define TYPE. Stands were classified as reproducing when the juvenile density class was 1 or greater (i.e., ≥ 5 individuals).

Celtis reticulata growth rate, expressed by site indices, was analyzed as the dependent variable in one-way analyses of variance (ANOVA) against the environmental parameters topographic position, parent material, soil texture, grazing intensity, and topographic shelter. Relationships between site indices and ordered categorical independent variables were analyzed by linear regression. With few exceptions, height site index was a more sensitive predictor of growth differences than diameter site index. *Celtis reticulata* growth rates and relationships with topographic position and other environmental parameters were also analyzed with analysis of covariance, to combine categorical and continuous factors. Included in the model was the categorical variable topographic position, with soil texture, topographic shelter, grazing intensity, and parent material as four covariates. Relationships between environmental variables and stand structure (TYPE) and the number of modes were analyzed by contingency tables and ANOVA.

RESULTS

Growth

Log-log regressions best represented the statistical relationship between height and age (Fig. 3) and diameter and age of *C. reticulata* individuals. An initial impression that regression lines do not fit the scatter of points at log(age) <1.2 can be reconciled by recognizing that the dense central elliptical clouds of points have controlled the regression results. In both cases the least-squares fit resulted in a good fit to the dense cloud of points representing middle-aged trees, but resulted in almost entirely negative residuals for trees younger than 10–25 yr. Because these younger trees were from a small number of sites, many of which showed battering by floods, distributions of residuals were judged to be acceptable.

Celtis reticulata diameter and height were tightly related in a log-log regression ($R^2 = .75$). Mean height and diameter of dominant and codominant *C. reticulata*, regardless of age, were 5 m and 18 cm, respectively. While diameter is a better predictor of age than height ($R^2 = .53$ and .25, respectively), height is more responsive to site characteristics than is diameter, both in the literature and in this study. Thus, height was the preferred basis for the site index.

Fifty-year-old *C. reticulata* trees in Idaho averaged 3.9 m tall and 13.6 cm in diameter. Using height, we constructed site index curves

TABLE 2. Categorization of the *Celtis reticulata* stand structure variable TYPE. TYPE represents the five types of stand structure that were recognized from the density classification. Within each stand, the three size classes of trees (juvenile, mature, decadent) were assigned to a density class based on the following definitions. Mid-point values were used as needed. **Juvenile**: (1) widely scattered—5 or fewer juveniles present; (2) scattered— >5 juveniles present in a nonaggregated distribution averaging >10 canopies apart; (3) subcontinuous—breaks in the total canopy exist but juveniles average >3 and <10 canopies apart. **Mature/Decadent**: (1) widely scattered—mature individuals >10 crown widths apart; (2) scattered—mature individuals separated by gaps of >4 and <10 individual crown widths; (3) subcontinuous—breaks in the total canopy exist but mature individuals average ≤ 3 crown widths apart; (4) continuous—mature trees form a continuous matrix with only occasional gaps.

		Density class		
TYPE	Description	Juvenile	Mature	Decadent
1	Young	≥ 1	≤ .5	≤ 2
2	Nonreproducing, nondecadent	≤ .5	>.5	≤ 2
3	Reproducing, nondecadent	≥ 1	≥ 1	≤ 2
4	Reproducing, decadent	≥ 1	≥ 1	>2
5	Nonreproducing, decadent	<1	>.5	>2

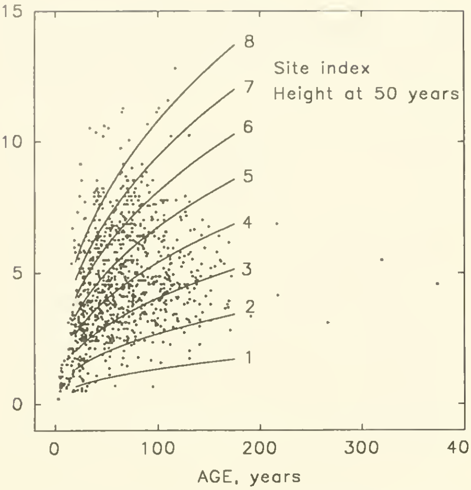

Fig. 3. Nontransformed log-log regression of *Celtis reticulata* height (m) on age and site index curves for the Idaho stands.

for Idaho *Celtis* stands to allow site classification for a stand at any age (Fig. 3). Site quality of an area can be assessed by determining average height and age of dominant trees and locating the position of these coordinates on the site index graph. The stand's site index is then read from the closest curve.

Site quality, as expressed by the height-based site index, differed among the eleven topographic positions identified ($P = .0001$, $F = 4.4$) (Table 3). However, variation within topographic positions was large, so that at the .05 significance level, only draws differed from any other specific topographic position. Growth was faster in draws than on talus slopes, upper slopes, mid-slopes, and stream terraces.

Although site index means did not differ statistically between most topographic positions, a relatively predictable biological ranking of topographic positions was expressed, with a general trend of faster growth where sheltered and mesic to slower growth on more xeric and exposed sites. For example, site index values were smallest on talus slopes, followed by upper slopes, mid-slopes, and stream terraces (Table 3).

Celtis reticulata occurred infrequently on north- and east-facing slopes (Fig. 4A). Twenty-five percent (60) of stands were found on SW slopes, with a heat load between 0.95 and 1.00, the hottest values of the heat load index; 58% (140) were between 0.74 and 1.00. Only 32 stands (13%) were located on the coolest sites between 0.00 and 0.20, or between 350° and 98° east of north. The mean heat load index was 0.69. No stands were found between 349° and 9° east of north.

In spite of *C. reticulata's* affinity for southerly exposures, heat load was not a good predictor of hackberry growth characteristics. More often than not, stands have an affinity for southerly exposures, but because of topographic sheltering, growing conditions are often not as harsh or water stressed as they first appear. Of 241 *Celtis* stands, 168 (70%) had at least an intermediate topographic shelter.

In a stepwise regression analysis from a pool of six independent variables (soil texture, rock, grazing intensity, shelter, heat load, and slope), shelter was the most important predictor of site index ($R^2 = .13$, $P < .001$, $F = 35.5$). Site index values were largest when shelter was greatest, with well-sheltered stands differing from intermediate and open exposures (Table 4). However, variability in growth rates within a given class of shelter is large, as shown by the low R^2.

Presence of *C. reticulata* is correlated with surface rock or rock outcrops. Of the 241 stands sampled, 96 (40%) had a surface rock cover of 50% or more (Fig. 4B). Twenty percent of the stands were extremely rocky, with rock covering 75–98% of the ground surface. Average rock cover was 39%.

A weak, inverse relationship between percent surface rock cover and site index was found ($R^2 = -.28$, $P = .0001$). As rock cover increased, site index tended to decrease slightly. Rock was a statistically significant variable in a stepwise multiple regression as well, following topographic shelter in order of entry. Including rock in the model increased the R^2 value from .13 to .20 ($F = 28.9$, $P < .001$). On sites classified as draws, where topographic shelter is maximized, surface rock cover is less important.

Neither parent material nor grazing intensity was a statistically significant predictor of site index ($P = .43$ and .14, respectively). However, site index values differed with soil texture ($P = .023$, $F = 2.07$). As with topographic position (Table 3), means were ranked by Fisher's LSD procedure in an intuitively predictable order. Growth rates were higher on finer-textured soils (clay or loam) than on coarse-textured soils (sand). At alpha = .05, the

TABLE 3. Site index values of *Celtis reticulata* (s = standard deviation) for each topographic position. Mean site index (SI) values have been transformed back into the original scale of measurement to aid interpretation. Topographic positions with no overlap of similarity grouping letters are different from each other at the .05 significance level (Fisher's LSD).

Topographic position	Mean SI: transformed (s)	Mean SI: back-transformed	N	Similarity grouping
Draw	0.74 (0.16)	5.5	30	A
High-water line	0.65 (0.15)	4.4	37	AB
Toe slope	0.61 (0.14)	4.1	17	AB
Rocky draw	0.58 (0.17)	3.8	15	AB
Lower slope	0.57 (0.19)	3.7	40	AB
Bench	0.56 (0.24)	3.6	16	AB
Broken lower slope	0.55 (0.12)	3.5	20	AB
Stream terrace	0.51 (0.31)	3.2	13	BC
Mid-slope	0.50 (0.18)	3.2	28	BC
Upper slope	0.48 (0.20)	3.0	12	BC
Talus slope	0.47 (0.13)	2.9	13	BC

only pairs that differed from each other were talus and loam.

Interactions between soil texture and topographic position were highly significant (Chi-square, $P = .001$). When the analysis of site index and soil texture was restricted to just upland sites, the effect was slightly more pronounced ($P = .014$, $F = 2.49$).

Growth Form

"Shrubbiness" was quantified by counting the number of live and dead main stems or trunks of each individual. Regression analysis of stem number with the variables grazing intensity, topographic shelter, soil texture, heat load, slope, average height, average diameter, and percent surface rock cover produced several statistically significant, albeit weak, relationships. Live and dead stem density per individual decreased as topographic shelter increased ($R^2 = .20$ and .30, respectively). Average height decreased slightly as the number of live stems increased ($R^2 = .20$). In general, on sheltered sites *C. reticulata* has a single stem (treelike) rather than multi-stem (shrublike) growth form.

Differences in plant growth form were found among topographic positions and among parent materials. Individuals growing at mid-slope were generally shrubbier, with a greater number of live stems ($\bar{x} = 2.5$), than individuals growing at high-water line ($\bar{x} = 1.4$), in draws ($\bar{x} = 1.6$), and in rocky draws ($\bar{x} = 1.5$) (ANOVA, $P = .003$, $F = 2.71$). Dead stems were far less numerous than live stems and were absent from most individuals. The number of dead stems at mid-slope ($\bar{x} = 0.6$) was greater than all other topographic positions except upper slopes ($P = .0001$, $F = 6.5$). Stands at high-water line, rocky draw, stream terrace, draw, and broken lower slope topographic positions averaged only 0.1 dead stems per individual. Growth form did not differ with the number of size modes within a stand.

Individuals on sandstone were more commonly multi-stemmed than those on the three other parent materials, for both living and dead stems ($P < .001$, $F = 8.5$; $P < .001$, $F = 14.7$, respectively).

Longevity

The mean age of individuals sampled during our study was 66 yr, with a range of 1–374 yr (Fig. 5). Old age and large size are not tightly related. For example, it is common to find trees 10 m tall but less than 75 yr old. Diameter was often a better predictor of age than was height ($R^2 = .54$ and .26, respectively, after log-log transformation).

The oldest *C. reticulata* recorded in this study (about 374 yr) grew on an exposed talus slope approximately 300 m above the Salmon River; it was 4.6 m tall and 48 cm in diameter at 20 cm above ground level. Percent surface rock cover of the site was 90%, with the small stand of scattered trees restricted to talus margins where pockets of soil were exposed. Other members of the stand ranged in age from 191 yr (3.35 m tall, 28 cm diam) to 320 yr (5.48 m tall, 46.5 cm diam).

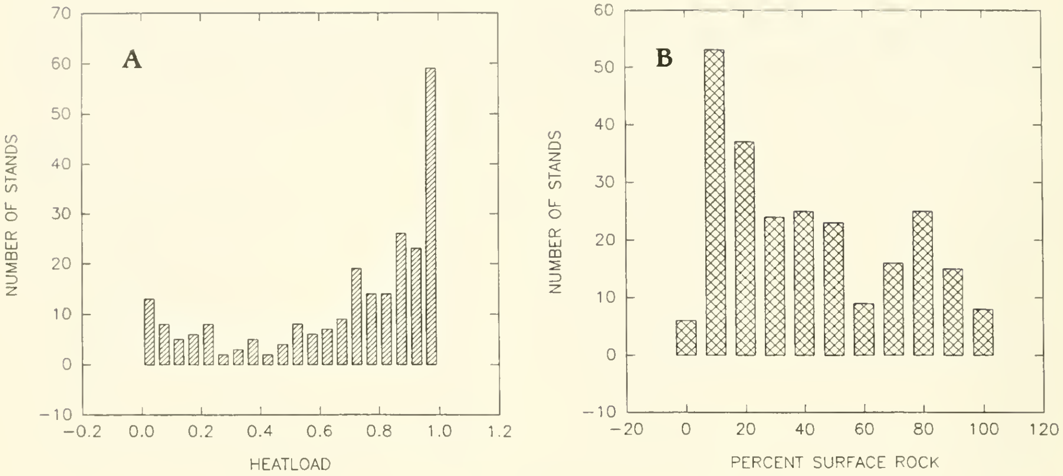

Fig. 4. Frequency distributions of the number of *Celtis reticulata* stands by (A) heat load and (B) percent surface rock cover.

Stand Structure

Of the 241 *Celtis* stands, 178 (74%) were reproducing and only 4 (1.7%) of these were decadent. Fifty-seven stands (23.5%) were classified as nonreproducing, 6 (2.5%) of them decadent. The remaining 6 stands (2.5%) were recently established (juvenile dominated), with no mature individuals present.

Structure of *C. reticulata* stands, in terms of their relative densities of juvenile and mature size classes, was unrelated to soil texture (Chi-square, $P = .31$). Structural type was weakly related to topographic position of the stand (Chi-square, $P = .08$). Of the 11 topographic positions, rocky draws had the highest juvenile density, or recruitment. In general, juvenile densities increased as the percent of surface rock cover increased. Density of *C. reticulata* juveniles was highest when rock cover was 50% or greater.

Rocky draws consistently had the densest canopies, followed by draws and high-water line. Rocky draws were never assigned an overall density <2.5, where 3 = subcontinuous. In fact, 75% of rocky draws had closed or nearly closed canopies (overall density = 3.5 or 4). Juveniles were often present on the margins of rocky draws.

The few decadent stands were found higher on the slope, on steeper slopes, and in less-sheltered positions than nondecadent stands. Nonreproducing, decadent stands were more steeply sloping than young and nondecadent, nonreproducing stands (ANOVA, $P = .003$, $F = 4.03$) (Table 5). Of the 10 decadent stands, 50% were at mid-slope and 20% were on talus.

While none of the decadent stands were extremely overgrazed, their distance from water may have confounded this result. Overgrazed stands were typically found on fairly gentle terrain ($\bar{x} = 14°$, S.D. = 8.6) and in close proximity to a water source, where livestock tend to concentrate, while decadent stands were on steeper slopes (Table 5) and at higher slope

TABLE 4. Mean site index (SI) values for *Celtis reticulata* for three levels of topographic shelter, in both transformed and back-transformed scales. Topographic shelters with no overlap of similarity grouping letters are different from each other at the .05 significance level (Fisher's LSD).

Topographic shelter	Mean SI: transformed (s)	Mean SI: back-transformed	*N*	Similarity grouping
Sheltered	0.69 (0.15)	4.9	73	A
Intermediate	0.55 (0.20)	3.6	129	B
Exposed	0.49 (0.14)	3.1	39	B

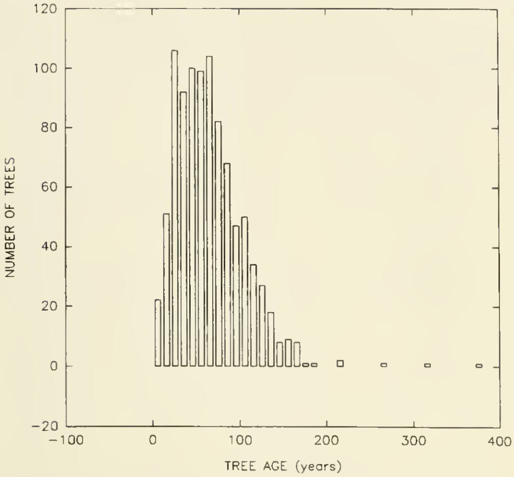

Fig. 5. Frequency distribution of the number of *Celtis reticulata* trees by tree age.

TABLE 5. Average slopes of decadent, nondecadent, and young stands of *Celtis reticulata*, with the variable TYPE in its original five-category format. TYPE represents the five types of *Celtis reticulata* stand structure that were recognized.

TYPE	N	Mean slope (degrees)	S.D.
Young (juvenile)	6	12	3.4
Nonreproducing, nondecadent	51	20	9.6
Reproducing, nondecadent	174	22	10.3
Reproducing, decadent	4	27	7.7
Nonreproducing, decadent	6	33	5.0

positions. Less intensively grazed stands averaged 23° (S.D. = 10.1).

Grazing level was related to stand structure (TYPE; Chi-square, $P = .0002$). A larger percentage of heavily grazed stands (53%) were nonreproducing than were stands with light or moderate grazing intensity (18.5%). Even though sample sizes were very different (light or moderate = 205, extreme = 36), the pattern confirms field observations of low recruitment under extreme grazing pressure. However, it is perhaps even more noteworthy that recruitment on heavily grazed sites is as high as it is, given how few, if any, other shrub species are present on such sites.

Among the four parent materials, 37% of *C. reticulata* stands growing on sandstone were nonreproducing, as compared to 21%, 22%, and 21% of stands growing on granite, basalt, and river alluvium, respectively (Chi-square, $P = .014$; Table 6). A greater number of sandstone-associated stands were nonreproducing than expected (14 and 9, respectively), while fewer were reproducing than expected (22 and 27, respectively). Expected and observed values for the three other parent materials were more similar.

Newly established *C. reticulata* stands are apparently rare, as few were observed during the study in spite of efforts to locate them. Only six young (<33 yr) stands were sampled. These were typically on rocky sites with intermediate topographic shelter and gentle slopes ($\bar{x} = 12°$). All had at least 15% surface rock cover, but most had 75% or greater rock cover ($\bar{x} = 65\%$). Five of the six stands were on alluvium, including stream terraces, high-water lines, and benches. All five had sandy soil. The sixth stand was atypical, occurring near a midslope, sparsely vegetated band of sandstone with intermediate shelter. All individuals were shrubby, decadent, and old (18–33 yr) relative to the average height of 0.7 m (expected age = 8 yr). Soils were sandy loam in texture.

While young stands were only on sites with intermediate topographic shelter, reproducing and nonreproducing stands differed little in the degree of shelter they received (Chi-square, $P = .06$). Thirty-three percent of reproducing stands were sheltered, compared to 25% of nonreproducing stands.

The amount of surface rock differed weakly across stand structure (TYPE; ANOVA, $P = .038$, $F = 2.58$). Differences were greater when the variable TYPE was restructured to three categories (mature reproducing, mature nonreproducing, young), eliminating decadence as a factor (ANOVA, $P = .015$, $F = 4.26$). Under the three-level categorization, young stands were rockier than mature, nonreproducing stands ($\bar{x} = 32\%$) but did not differ from those that were reproducing.

Number of Modes

Celtis reticulata stands typically appeared to be unimodal (73%), with one dominant cohort. Stands with two modes were far less common (11%), but a slightly greater number were all-aged (16%). Since only two stands had three modes, they were dropped from analyses;

TABLE 6. Cross tabulation of the number of *Celtis reticulata* stands by stand structure and parent material. The hypothesis of independence of stand structure and parent material is rejected with $P = .014$.

Parent material	Observed/ expected	Mature		Young	Row total	Row %
		Nonreprod.	Reprod.			
Granite	obs.	11.0	40.0	0.0	51	21
	exp.	12.2	37.6	1.3		
Sandstone	obs.	14.0	22.0	1.0	37	16
	exp.	8.8	27.2	0.9		
Basalt	obs.	20.0	71.0	0.0	91	38
	exp.	21.5	66.3	2.3		
Alluvium	obs.	12.0	45.0	5.0	62	25
	exp.	14.5	44.9	1.5		
Column total	obs.	57.0	178.0	6.0	241	100
Column %		24%	74%	3%		

thus, the sample size for this portion of the results is based on 239 stands. Growth form or number of stems of the individuals was unrelated to number of modes.

Although of marginal statistical significance, all-aged stands were more common on sheltered sites (Chi-square, $P = .07$). For example, 33% of stands in draws, which typically have at least an intermediate topographic shelter, were all-aged. The percent of all-aged stands at other topographic positions ranged from 6% to 16%.

Livestock grazing intensity may restrict entry of new cohorts within a *C. reticulata* stand as shown by the strong tendency for overgrazed stands to be unimodal (92%; Chi-square, $P = .0008$). In contrast, 70% of light to moderately grazed stands had only one mode, 11% were bimodal, and 18% were all-aged.

Size structure of *Celtis* stands did not differ with topographic position, parent material, soil texture, slope, percent surface rock, or heat load (all $P > .2$).

DISCUSSION

In our study, trees were typically tallest and least shrubby when located in draws, on sites with surface or subsurface moisture, and in areas where they received maximum topographic shelter. Similar observations of *C. reticulata* have been recorded by others (Eliot 1938, Van Dersal 1938, Peattie 1953), and for different species of *Celtis* as well. For example, Hitchcock and Cronquist (1964) noted that *Celtis reticulata* is taller in moist areas in the Pacific Northwest. In Oklahoma, *C. laevigata* (sugarberry) is typically a small tree in open areas, but in lowland forests it reaches its maximum development (Schnell et al. 1977). On the eastern Great Plains, *C. tenuifolia* (dwarf hackberry) is a gnarled, shrublike tree when growing on its typical rocky, shallow, calcareous substrate, but in the bottom of ravines it may reach heights of 8–10 m (Stephens 1973). In addition to the influence of an ameliorated environment, sheltered stands may be less prone to repeated disturbances such as fire, to which a vegetative sprouter such as *C. reticulata* will often respond with a shrubbier growth form.

In Oklahoma, *Celtis* occurs almost exclusively on loamy bottomland soils (Dooley and Collins 1984), and in west Texas it is best developed on alluvium (Van Auken et al. 1979). In the canyon grasslands of Idaho, Tisdale (1986) recognized two types of *Celtis*-dominated vegetation on soils of two principal origins. The *C. reticulata–Agropyron spicatum* habitat type occurs on lower valley slopes with rocky (50–60%), weakly developed loam soils derived from residual and colluvial materials. The second vegetation type, unclassified because of heavy livestock disturbance and alien plant dominance of the understory, occurs on alluvial terraces with deep sandy soils.

Soil texture appears to have a greater influence on *C. reticulata* growth on upland sites than on sites associated with a perennial water source. While *C. reticulata* grows on a range of soil textures in Idaho, we found the tallest trees on loams, possibly because of their greater water-holding capacity and nutrient content. However, 80% of the stands occurred on soils with some sand component, and 30% were on sand or coarse sand. The presence of good drainage may be an important limiting factor for *C. reticulata,* as finer-textured soils of the uplands were nearly always skeletal. The increased percolation of sandy or skeletal soils provides greater moisture availability for deep-rooted shrub and tree species.

In Idaho, *C. reticulata* is most prevalent on rocky sites with southeast to westerly aspects, although heat load was not an important predictor of growth. The presence of rock, particularly bedrock, may in fact be critical for hackberry's existence on certain sites. It may also partially explain the fragmented distribution of the species in Idaho. Other rock-associated species have been observed in semiarid regions as well. In the shrub-steppe region of eastern Montana, Rumble (1987) found that scoria rock outcrops provide a unique habitat for several relatively mesic species. *Rhus trilobata* (skunkbush sumac), *Prunus virginiana* (chokecherry), *Ribes* spp. (currant), and *Juniperus* spp. (juniper) were found only in association with rock outcrops in that ecosystem. He concluded that their occurrence is probably related to protection from wind, snowdrift accumulation, shading, and mulch effects of rocks. Oppenheimer (1964) and Potter and Green (1964) suggested that the association of mesic species with rocky substrates is due to temporary water reservoirs that rock fissures provide. In Arizona, Johnsen (1962) reported that *Juniperus monosperma* (one-seed juniper) is largely limited to rock outcrops, where he recorded 2–2.5 times as much available moisture. The theory of extra moisture availability in rock fissures could also hold true for the deeply rooted *C. reticulata,* helping explain its frequent presence on southerly aspects.

Other plausible explanations for the infrequency of *C. reticulata* on northerly aspects and sites with less surface rock cover include its sensitivity to late spring frosts (personal observation) and poor competitive ability with fast-growing species. In Idaho, *C. reticulata* is the last shrub to break dormancy and expand its leaves in the spring. This strategy, in combination with the tendency to grow on warmer slopes, generally prevents frost damage from occurring. The greater effective soil moisture and dense vegetative cover of north slopes probably create an environment too competitive for this slow-growing species.

In summary, *Celtis reticulata* can generally be described as slow-growing and small-statured. Fifty-year-old trees averaged 4 m tall and 13.6 cm in diameter in Idaho, with a mean tree height and diameter, regardless of age, of 5 m and 18 cm, respectively. Unlike some shrub and tree species in the Intermountain West, populations are generally maintaining themselves by vegetative sprouting or seedling recruitment, despite historic and prevailing large-scale habitat alterations resulting from overgrazing, exotic plant invasion, and changing fire frequencies (Tisdale 1986, Whisenant 1990). Hackberry's general resiliency and ability to resprout following disturbance or injury likely play a role in this, as does its positive association with rock. Recruitment, as expressed by the density of juvenile individuals, increased as surface rock cover increased. However, under extreme grazing pressure, recruitment was significantly lowered and stands were nearly all unimodal. All-aged stands were absent from severely grazed sites. Even though rock favors *Celtis* recruitment, its growth is favored on less-rocky sites, such as draws.

The most likely explanation for relatively slow *C. reticulata* growth on stream terraces, in spite of the assumed availability of groundwater, is the extreme annual fluctuation of the water level and battering by flood debris. These sites are located below the high-water line. Above the high-water line the mean site index is larger and mechanical stresses are less extreme. While newly established *C. reticulata* stands were uncommon, they typically occurred on these riparian sites, where establishment conditions occur more frequently than in the uplands.

Although individuals are often slow-growing, the variation in site conditions that the species appears to tolerate and its other positive attributes (i.e., wildlife food, cover, landscape structure, potential large size, tolerance of southerly aspects), are favorable qualities for those seeking rehabilitation species. The species' persistence in heavily degraded ecosystems may speak to its suitability for rehabilitation projects as well.

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MIMULUS EVANESCENS (SCROPHULARIACEAE): A NEW ANNUAL SPECIES FROM THE NORTHERN GREAT BASIN

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ABSTRACT.—Recent taxonomic studies in *Mimulus* support the recognition of *Mimulus evanescens*, a new autogamous species morphologically allied with *M. breviflorus* and *M. latidens*. Initially known only from herbarium specimens, the most recent from 1958, *M. evanescens* was relocated in the field in 1990 in northern Lassen Co., CA. A second population was found in southern Lake Co., OR, in 1993. *Mimulus evanescens* is apparently confined to the Great Basin and its periphery, where it has been recorded from 10 localities across Idaho, Oregon, and California. Based on collection information and visits to the two extant populations, the new species appears to be restricted to vernally moist sites and fluctuating banks of intermittent streams or pools. Long-term utilization of such sites by livestock may have contributed to the present-day rarity of *M. evanescens*. The species should be added to federal and state lists of candidate endangered species pending the results of future field studies and surveys.

Key words: Mimulus, *Great Basin, taxonomy, Scrophulariaceae, monkeyflower,* Mimulus breviflorus, Mimulus latidens.

Mimulus breviflorus is a diminutive, self-pollinating, annual monkeyflower occurring primarily east of the Sierra Nevada and Cascade Mountains in the northwestern United States and adjacent British Columbia. Little is known concerning the evolutionary or taxonomic relationships of this or most other taxa in the genus, which comprises perhaps 100 predominantly North American species (Thompson 1993). In the only comprehensive monograph of the genus, Grant (1924) placed *M. breviflorus* in section *Paradanthus*, an assemblage of small, problematic species groups that are probably paraphyletic and considered difficult to align taxonomically (Argue 1980). Indeed, in a proposed phylogenetic chart Grant (1924) affiliated the yellow-flowered *M. breviflorus* with the *M. moschatus* alliance, while in the text of her paper she associated the species with members of the *M. inconspicuus* group, particularly the white- to pinkish-flowered *M. latidens* of California.

The proposed relationship between *Mimulus breviflorus* and *M. latidens* is largely based on shared features of the corolla and calyx. Both species possess short, inconspicuous corollas and strongly plicate, chartaceous fruiting calyces that inflate with age. Although inflated calyces are also described for some members of the *M. moschatus* complex (Grant 1924, Munz 1959, Holmgren 1984), the consistently reduced, essentially regular flowers of *M. breviflorus* and *M. latidens* are unlike any species in that group. The calyx morphology and texture of the two species is also different, being singularly reminiscent of *M. inconspicuus* and its proposed relatives (Grant 1924). Moreover, the general habit of *M. breviflorus* and *M. latidens* is more comparable to this group than to any other.

Despite the similarities, *Mimulus breviflorus* and *M. latidens* are quite distinct with respect to geography and habitat. *Mimulus breviflorus* is a basin and range species, principally occurring in well-drained, rocky environments near rain pools, rocky meadows, and ephemeral streamsides, often at middle and upper elevations. It has rarely been recorded south of extreme northeastern California, and only then above 2000 m. *Mimulus latidens* occurs mostly on poorly drained flats or slopes subject to vernal inundation, primarily below 800 m. The species is virtually endemic to California, extending from the Central Valley to northern Baja California. The apparent uncertainty by Grant (1924) over the taxonomic placement of *M. breviflorus* may have been influenced by geography, in that the range of the species overlaps much of the *M. moschatus* complex but not *M. latidens* or the *M. inconspicuus* group, which are restricted to cismontane California.

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The present study was prompted by several unusual herbarium collections identified as *Mimulus breviflorus*, discovered during a taxonomic survey of the *Mimulus washingtonensis* complex (Meinke in preparation) in which several hundred collections (including all relevant types) were examined. Despite the evidently yellow flowers and the fact that the few collection localities were well within the known range of *M. breviflorus*, the plants were similar to *M. latidens* in many respects. The anomalous material originated from several scattered stations across the upper Great Basin and its northern periphery, all within areas believed historically grazed by livestock. The most recent of these collections is dated 1958, and there was concern that the entity may have become extinct in the interim. Unexpected opportunities to observe living populations in the field were presented in 1990 and 1993 during chance visits to two reservoirs in Lassen Co., CA, and Lake Co., OR. The unique and consistent combination of features noted in herbarium collections, including bright yellow corollas, was even more conspicuous in living plants, prompting a taxonomic reevaluation of their relationship with *M. breviflorus* and *M. latidens*. After further evaluation, the unusual populations were considered to represent a new species which is here described, illustrated, and contrasted with potentially related taxa.

DESCRIPTION OF THE SPECIES

Mimulus evanescens **Meinke, sp. nov.** (Figs. 1A–C).—TYPE: USA, California, Lassen Co., 20.5 km east of Adin, north side of Ash Valley Rd., ca 0.1 km east of the Lassen National Forest boundary, in broken boulders and heavy gravel abutting Moll Reservoir, T38N R10E, NW1/4 SW1/4, Sect. 25, ca 1500 m, 27 June 1990, *Meinke and Kaye 5900* (holotype, OSC; isotypes, MO, NY, RM, UC, US, UTC).

Herbae annuae, puberulentes, ± viscido-villosae; *caulis* tenuis, erectis, (6–)10–25 cm altis, internodiis elongatis; *foliis* late ovatis vel lanceolatis, lamina integerrima vel parce denticulata, acuta, 1.0–3.8 cm longa, 0.7–2.9 cm lata, 3(–5) nervis, base lata, sessili vel subsessili; *pedicel* foliis brevioribus, tenuibus, ascendentibus; *calyce* in statu florifero 3.5–6.5 mm longo, 1.5–3.5 mm lato, in statu fructifero late urceolato, 7.0–11.0 mm longo, 5.0–8.5 mm lato, valde glabro, dentibus ciliati, late triangularibus, ± subaequalibus, acutis; *corolla* flava, brevi, 4.0–9.5 mm longa, calyce ca 1.5 plo longiore, tubo incluso, lobis ± aequalibus, patulis, erectis; *staminibus* stylo aequalibus, inclusis, glabris; *stylo* glabro, 3.0–7.8 mm longo, labiis stigmatis laciniatis, subaequalibus; *capsula* inclusa, subglobosa, 4.8–9.0 mm longa, sessili vel substipitata; *seminibus* late oblongis, ca 0.3–0.6 mm longis.

Annual herb, ± succulent, glandular-puberulent throughout (except the calyces), the hairs short and appearing of even length to the naked eye, moist or slimy to the touch, mostly one-celled (excluding the gland); *stems* slender, (6–)10–25 cm tall, erect to slightly decumbent in robust individuals, simple or branched from near the base, often sparingly branched above as well, with elongated internodes; *leaves* acute, broadly ovate to somewhat lanceolate, 1.0–3.8 cm long, 0.7–2.9 mm wide, evenly distributed, not much reduced at the upper nodes, not forming a basal rosette, the lower ones abruptly petiolate or subsessile, petioles 1–3 mm long, blades broadly sessile above, with 3(–5) primary veins, the margins entire or shallowly denticulate; *pedicels* slender, 8–18 mm long, ascending in flower and fruit, shorter than the leaves in fruit or longer in depauperate individuals; *inflorescence* racemose, flowers axillary; *flowers* inconspicuous, autogamous; *calyx* 3.5–6.5 mm long and 1.5–3.5 mm wide in flower, tubular-campanulate at anthesis, green becoming stramineous and anthocyanic along the angles with age, accrescent and broadly urceolate to oval in fruit, 7.0–11.0 mm long and 5.0–8.5 mm wide, the tube chartaceous and glabrous, the orifice narrowing and becoming somewhat oblique, the angles strongly plicate, the teeth broadly triangular, acute, 0.8–1.6 mm in fruit, ciliate on the margins, scarcely unequal, the uppermost lobe occasionally appearing slightly longer in some flowers; *corolla* short and essentially regular, 4.0–9.5 mm long, clear yellow or occasionally with a few tiny brownish dots in the throat, the inconspicuous petal lobes rounded or mucronate, the tube included or barely exserted, the limb exceeding the calyx by 2–3 mm, lobes short and subequal, mostly erect, glabrous externally, bearded internally with a few ± clavate hairs extending in a line from the lower palate into the floral tube;

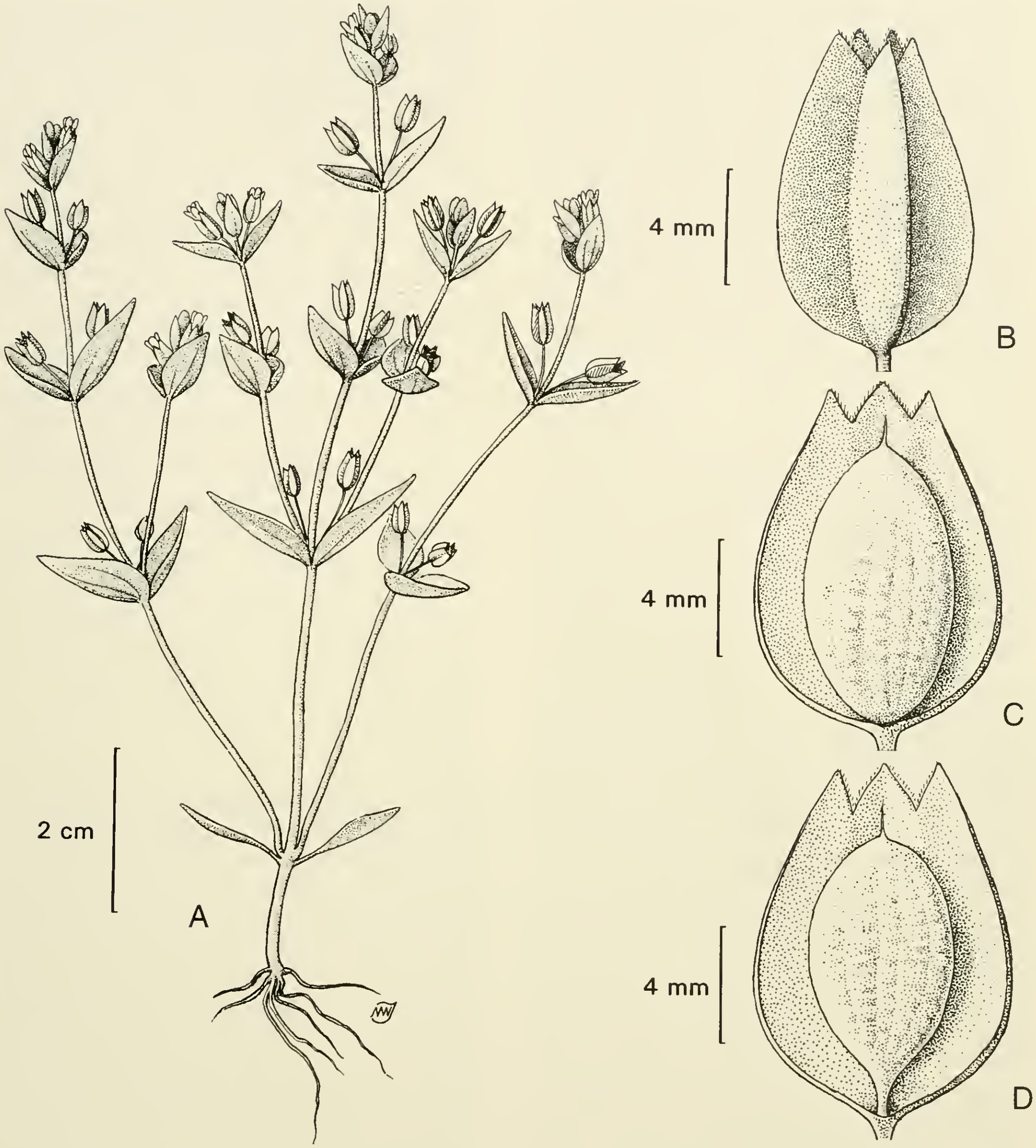

Fig. 1. *Mimulus evanescens* Meinke: A, habit drawing showing details of leaf morphology, inflorescence, and relationship between pedicel and leaf blade length; B, close-up of fruiting calyx of *M. evanescens*; C, calyx of *M. evanescens* opened to show sessile capsule insertion; D, calyx of *M. latidens* opened to show stipitate capsule insertion.

stamens included, about equal with the style, glabrous, pale; *style* glabrous, included, 3.0–7.8 mm long, stigma lips equal or subequal, shallowly laciniate-margined; *capsule* included, subglobose, 4.8–9.0 mm long, extending to ca 1.0–2.5 mm below the sinuses of the calyx teeth, sessile, or rarely with an abbreviated stipe up to ca 0.5 mm long, the placentae adherent to the apex; *seeds* ovoid or broadly oblong, brownish, 0.3–0.6 mm long, dormant when first ripe, dispersal often delayed or prolonged due to the nearly closed, inflated calyx.

PARATYPES.—**USA, California,** Lassen Co., 10 mi south of Ravendale, 9 June 1940, *Pennell 25763* (P); 4.8 mi south of Madeline, 17 June 1958, *Raven and Solbrig 13298* (JEPS); Modoc Co., along Willow Creek, June 1894, *Austin s.n.* (UC). **Idaho,** Owyhee Co., meadow, 3 mi south of Riddle, 1 July 1949, *Holmgren and Holmgren 7973* (CAS, UC, WS, WTU). **Oregon,** Crook Co., Grizzly Butte, 18 June 1894, *Leiberg 275* (NY, ORE, US); Gilliam Co., forks of Cottonwood Canyon, 6 June 1894, *Leiberg 156* (NY, ORE, P, US); Grant Co., Ochoco National Forest, Graylock Butte, 6 July 1912, *Ingram s.n.* (RM); Harney Co., dry watercourse near Frenchglen, 26 June 1942, *Peck 21389* (CAS, NY, P, UC, WILLU); Lake Co., moist to muddy margins of receding water, among rocks, Drews Reservoir, 15 June 1993, *Meinke and Carlson 6401* (BRY, HSC, NY, OSC, RM, RSA, SRP, UC, US, UTC, WS, WTU).

DISTRIBUTION AND HABITAT.—*Mimulus evanescens* is distributed widely along the northwestern edge of the Great Basin at elevations of ca 1200–1700 m, ranging from southwest Idaho west through eastern Oregon and south into northeastern California. *Mimulus breviflorus* is more widespread and considerably more common. Although inconspicuous even when in bloom, it has been recorded from numerous collections located throughout much of the northwestern United States east of the Sierra Nevada and Cascade ranges. Outlying populations are known from southern British Columbia and south (rarely) to the mountains near Lake Tahoe. *Mimulus breviflorus* has a broader elevational range than *M. evanescens*, occurring from roughly 300 to 2900 m.

Mimulus latidens is essentially a California endemic, distributed below 800 m from the northern Central Valley south to San Diego. The most southerly populations are known from northern Baja California, while four historic collections from extreme southwestern Oregon, originally identified as *M. breviflorus*, represent the northern range limits. A recently discovered Great Basin population of *M. latidens*, occurring at ca 1700 m in southern Lake Co., OR (Shelly 1986), is noteworthy as it is the single recorded locality in which the range of this otherwise low-elevation species overlaps either *M. evanescens* or *M. breviflorus*. The population was persisting over several acres in a sagebrush-dominated swale as of 1993. This area is along the flyway for various waterfowl species migrating northeast across the Great Basin from central California.

The habitat of *Mimulus evanescens* can be evaluated only from the two extant localities, the first adjacent to Moll Reservoir in Lassen Co., CA, and the second at Drews Reservoir in Lake Co., OR, both occurring within sagebrush-juniper–dominated vegetation zones. Plants at both sites were scattered among rock fragments and alongside small boulders, in moist, heavy gravel that had been inundated earlier in the spring. The California population was discovered in 1990 and visited again in 1991, while the Oregon population was first located in 1993. Associated species during these years (for both locations) included *Artemisia tridentata, Juniperus occidentalis, Mimulus floribundus, M. suksdorfii, Porterella carnosula, Collinsia grandiflora, C. parviflora, Downingia* sp., *Mimetanthe pilosa, Heterocodon rariflorum, Poa bulbosa*, and *Bromus* spp. The perennials *Machaerocarpus californicus* and *Marsilea vestita* were common along the shoreline at the Lassen Co. site. Remaining locations for *M. evanescens* are known only through scanty herbarium labels, with specimens reportedly taken from rocky stream banks or drying watercourses. *Mimulus breviflorus* occurs in comparable microsites, frequenting wet, rocky sites that often dry out by late spring or early summer, as well as lush, gravelly meadows.

MORPHOLOGICAL COMPARISONS.—Monkeyflowers are often phenotypically plastic, and related annual species in particular may be subject to overlapping morphological variation depending on ecological conditions. In an attempt to objectively evaluate the phenetic relationships of the new species and its most similar congeners, a data set was compiled by scoring 18 vegetative and reproductive character states (Table 1) from 114 *Mimulus* collections representing 38 populations. Measurements were taken from 15 populations each of *M. latidens* and *M. breviflorus*, and 8 of the 10 extant and historical populations of *M. evanescens*. Three plants were measured per collection to provide population averages for each quantitative trait. Sample populations of *M. latidens* and *M. breviflorus* were selected from herbarium collections encompassing the geographic range for each species. Every effort was made to choose individuals of the three species that, based on field experience of the author, represented normally developed plants (i.e., not drought-stressed) from approximately the same life-history stage. Measurements were made on randomly selected individuals where possible, insofar as the limited number of phenologically acceptable collections permitted.

TABLE 1. List of morphological traits measured from *Mimulus* plants for use in principal components analysis. Thirty-eight study populations were sampled, including 15 each for *M. latidens* and *M. breviflorus*, and 8 for *M. evanescens*. An average measurement was derived for each trait (from 3 samples per population) for use in the analyses.

(1) Presence or absence of a basal rosette
(2) Length of initial stem leaf
(3) Width of initial stem leaf
(4) Length of upper cauline leaf
(5) Width of upper cauline leaf
(6) Base of upper cauline leaf (sessile versus distinctly petiolate)
(7) Peduncle length (in fruit)
(8) Calyx length (in fruit)
(9) Calyx width (in fruit)
(10) Length of calyx teeth (in fruit)
(11) Overall corolla length
(12) Corolla color (yellow versus rose, whitish, or ochroleucous)
(13) Length of lower corolla lip
(14) Width of lower corolla lip
(15) Length of capsule
(16) Width of capsule
(17) Capsule insertion (base sessile versus distinctly stipitate)
(18) Stem and leaf pubescence (clearly glandular-puberulent versus glabrous or subglabrous)

The data set was initially used to analyze morphological relationships between *Mimulus evanescens*, *M. latidens*, and *M. breviflorus* using a principal components analysis (PCA). Clustering relationships of sample populations were compared along the first two axes of variation and graphically displayed. As a second measure of overall dissimilarity, canonical discriminant analysis (DA) was performed on the same populations using only the quantitative characters from Table 1 (i.e., eliminating traits 1, 12, 17, and 18). On herbarium specimens the resolution of certain qualitative traits, such as flower color and degree of pubescence, may be open to interpretation if specimens are poorly preserved or mishandled after collection. Since many of the available *Mimulus* collections were old or otherwise less than optimal for a morphometric study, the potential existed for errors in judgment of qualitative traits to bias the analysis. As an alternative, DA was utilized to determine whether the elimination of diagnostic qualitative traits would result in a weaker phenetic relationship than that indicated by PCA. The multivariate statistical package in STATGRAPHICS (v. 4.0) was used for the two analyses.

PCA clustered the 38 populations into three well-defined groups conforming to a priori determinations of samples as *M. evanescens*, *M. latidens*, or *M. breviflorus* (Fig. 2). The first two principal components accounted for 88% of total variance (Table 2), indicating that the PCA scatterplot (Fig. 2) is a good gauge of overall morphological differences among the three species. DA resulted in a comparable pattern, although *M. evanescens* clustered somewhat closer to *M. latidens* when qualitative characters were excluded (Fig. 2). In both analyses, *M. evanescens* is clearly and consistently intermediate to *M. latidens* and *M. breviflorus*.

Upon first inspection *Mimulus evanescens* appears to be merely a robust version of *M. breviflorus*. The yellow, nearly regular corollas, essentially nonstipitate capsules, and short-puberulent foliage and stems are traits that are virtually identical in the two species. Since *M. evanescens* also develops papery, inflated fruiting calyces, which is the most prominent feature in most specimens of *M. breviflorus*, it is understandable that the identity of the new species has been obscured. However, the oversized habit of *M. evanescens* is striking, and all floral and vegetative characteristics average larger than in *M. breviflorus*.

The significance of these proportional differences was first noted when fresh material of *M. evanescens* from the type locality was compared with greenhouse-grown plants of *M. breviflorus*. Although many individuals of the new species suffered from insect predation in the field and others appeared underdeveloped due to drought, undamaged plants from moist microsites commonly grew to 2 dm or more, far exceeding the largest examples of *M. breviflorus*. Conversely, *M. breviflorus* plants cultivated in the greenhouse (originating from three distinct populations in eastern Oregon) never exceeded 12 cm in height. Rather than growing taller with age, they tended to branch out and become unusually floriferous. This observation was confirmed when plants of *M. breviflorus* and *M. evanescens* (32 and 27 individuals, respectively, from populations in Lake Co., OR) were grown together from seed in a common greenhouse environment. Given identical conditions, all *M. evanescens* plants grew to over twice the size of *M. breviflorus*. In addition, all quantitative and qualitative differences for the species originally noted on the

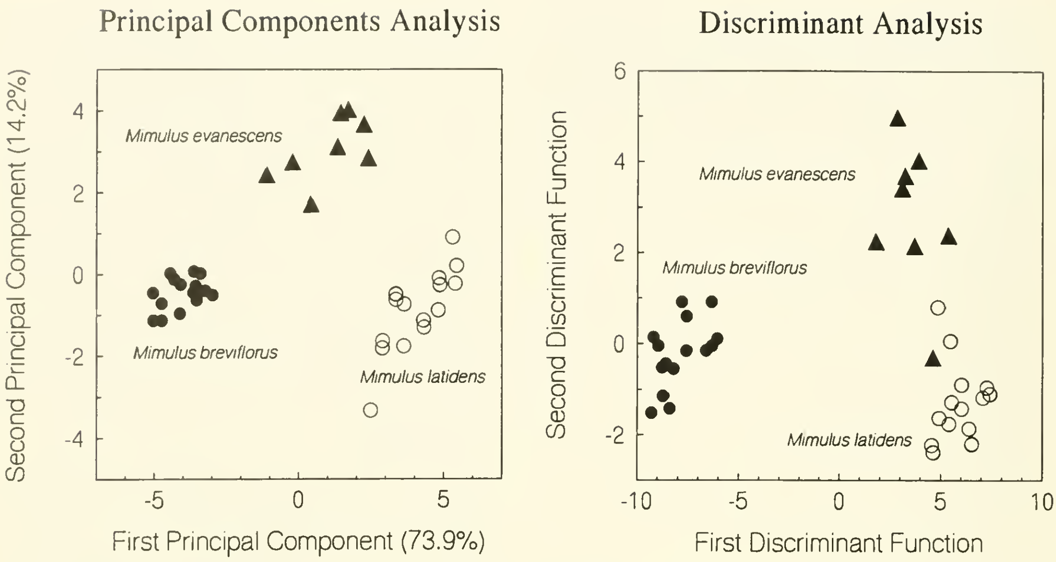

Fig. 2. Morphometric evaluations (see text for discussion): two-dimensional plots depicting principal components (18 qualitative and quantitative characters) and discriminant analyses (14 quantitative characters), contrasting the morphological relationships of *M. evanescens* (triangles), *M. latidens* (open circles), and *M. breviflorus* (closed circles).

herbarium specimens were maintained in culture. Although some herbarium specimens of *M. evanescens* are not particularly large, it is suspected that this is due to moisture limitation rather than genetic potential, based on observations of living plants.

In addition to the overall size disparity, other features readily separate *Mimulus evanescens* from *M. breviflorus*. Most evident are the leaves, which are ovate to broadly lanceolate in the new species and rhombic-ovate or narrowly lanceolate in *M. breviflorus*. Moreover, only the very lowest leaves of *M. evanescens* are petiolate, and these abruptly so (Fig. 1A), while leaf blades of *M. breviflorus* narrow gradually into slender, evident petioles at all nodes. In fruit, the pedicels of *M. breviflorus* generally exceed or at least equal the leaf blades. Those of the new species are always shorter in well-developed plants, and in some instances the leaf blade exceeds the calyx as well. Finally, the fruiting calyx of *M. evanescens* is much more plicate and typically exceeds the length of the mature capsule by 1.5–3.0 mm (Figs. 1B,C). In *M. breviflorus* ripe capsules are approximately the same length as the calyx. The overall dimensions of *Mimulus evanescens*, as well as the strongly angled fruiting calyx and broad, sessile leaves, are traits that also imply a relationship with *M. latidens*. There are substantial differences between these taxa, however, including flower color, pedicel length in relation to leaf length, stem pubescence, capsule insertion (Figs. 1C,D), and the presence of a basal rosette in *M. latidens*. Dissimilarities among the three species are summarized in Table 3.

TABLE 2. Amount of total variance accounted for by each principal component, in a principal components analysis of morphological variation among populations of *Mimulus evanescens*, *M. breviflorus*, and *M. latidens*.

Component number	Percent of variance	Cumulative percentage
1	73.88	73.88
2	14.18	88.06
3	3.75	91.81
4	2.41	94.22
5	2.12	96.34
6	1.22	97.56
7	.57	98.13
8	.46	98.59
9	.39	98.98
10	.29	99.27
11	.21	99.48
12	.17	99.65
13	.12	99.78
14	.11	99.89
15	.06	99.95
16	.05	100.00

TABLE 3. Diagnostic features of *Mimulus evanescens*, *M. breviflorus*, and *M. latidens*.

Character	*M. evanescens*	*M. breviflorus*	*M. latidens*
Plant height	(6–)10–25 cm	3–10(–14) cm	10–26 cm
Pubescence	Glandular-puberulent	Glandular-puberulent	Subglabrous
Basal rosette	No	No	Yes
Leaf base	Petiolate at base, sessile above	Petiolate throughout	Petiolate at base, sessile above
Leaf blade shape	Ovate to lanceolate	Elliptic-lanceolate	Broadly ovate
Cauline leaf length	1.0–3.8 cm	0.4–1.7 cm	0.8–3.2 cm
width	0.7–2.9 cm	0.2–0.5(–0.8) cm	0.5–1.7 cm
Pedicels	0.8–1.8 cm long, < the blades	0.5–1.9 cm long, > the blades	1.0–3.3 cm long, > the blades
Fruiting calyx length	7–11 mm	4–8 mm	9–12 mm
width	5.0–8.5 mm	3.0–4.5 mm	6–8 mm
Corolla color	Yellow	Yellow	Whitish, shaded rose or yellow
Corolla length	4.0–9.5 mm	3.5–5.5 mm	9.0–11.5 mm
Capsule insertion	± sessile	± sessile	clearly stipitate
Capsule length	4.8–9.0 mm, clearly inserted	4.5–8.0 mm, about equaling calyx	6.0–9.0 mm, clearly inserted
Distribution	Great Basin and vicinity	Great Basin and vicinity	Cismontane California
Elevation	~1200–1700 m	300–2900 m	≤800 m

Other small-flowered annuals that might be confused with *Mimulus evanescens* are primarily members of the *M. moschatus* complex, particularly *M. floribundus*, *M. patulus*, and *M. pulsiferae*. Of these, only *M. floribundus* is ever characterized as having an inflated fruiting calyx (Grant 1924), which can be distinguished from *M. evanescens* by the multicellular pubescence throughout and narrow, lanceolate sepals. These three species are further differentiated from *M. evanescens* by distinctly petiolate upper leaves and bilabiate corollas. Depauperate annual forms of *M. guttatus* also occur in moist sites within the range of *M. evanescens*. This common yellow-flowered species can be separated by petiolate upper leaves and strongly zygomorphic corollas. Although the calyces of *M. guttatus* are also markedly inflated, they are distinctly irregular and oriented horizontally in fruit. *Mimulus suksdorfii* is the only other annual monkeyflower in the Pacific Northwest with features comparable to *M. evanescens*. Seldom exceeding 6 cm in height, this compact, freely branched species is easily distinguished by obtuse, linear-oblong leaves, a cylindrical fruiting calyx, and flaring, emarginate corolla lobes.

PHYLOGENETIC CONSIDERATIONS.—Judging from morphology, *Mimulus evanescens* appears most closely related to *M. breviflorus* and *M. latidens*, and exhibits characteristics of both taxa (Fig. 2). *Mimulus latidens*, in turn, also seems to have a strong affinity to *M. inconspicuus*, *M. grayi*, and *M. acutidens* from California, based primarily on flower color, stipitate capsules, calyx morphology, leaf shape, and glabrous habit (Grant 1924, Thompson 1993). Aside from general vegetative and floral similarities, the inflated, plicate fruiting calyx is the principal trait linking these six species together. Whether or not this feature implies a monophyletic group is open to debate, however, since inflated calyces have evidently arisen independently in *Mimulus* on more than one occasion. Nonetheless, the shape and texture of the calyces of these species are distinctive.

The recognition of *Mimulus evanescens* allows for a reevaluation of the relationship between *M. breviflorus* and the rest of the genus. The morphology of *M. evanescens*, transitional between *M. breviflorus* and *M. latidens*, suggests that the new species might have arisen through hybridization. However, this hypothesis conflicts with the current geographical and ecological separation of the putative parents and the fact that *M. breviflorus* is highly autogamous. An alternative scenario proposes *M. evanescens* as a descendant of *M. latidens*. The smaller-flowered and apparently more successful *M. breviflorus* (based on the number of historic collections) may have then arisen from *M. evanescens*, perhaps as a result of a shift to more xeric conditions in what is now the Great Basin. *Mimulus breviflorus* is ubiquitous and well represented in herbaria while *M. evanescens* is apparently rare and widely scattered, providing circumstantial support for this concept. The discovery of the disjunct *M. latidens* population in Lake Co., OR (Shelly 1986) is intriguing, because it suggests a mechanism by which this relationship might have developed. If genotypes of *M. latidens* capable of survival outside of California's relatively benign Central Valley have been historically transported to the Great Basin by migrating ducks or geese, the means and opportunity for adaptive radiation could have existed.

CONSERVATION.—It is not encouraging that only 10 extant or historical populations of *Mimulus evanescens* are known, with only two sites recorded since 1958. This contrasts with hundreds of collections at dozens of localities for the much less conspicuous *M. breviflorus*. As with *M. breviflorus*, the distribution of *M. evanescens* is apparently limited to damp or wet sites at moderate elevations within open rangeland. Virtually all such sites in the Great Basin are associated with a long history of grazing by domestic livestock. The broad geographic range and relatively unremarkable habitat of *Mimulus evanescens* imply that the comparative rarity of the species may be the result of habitat loss or disturbance. However, the paucity of herbarium records, especially when contrasted with similar species, suggests that *M. evanescens* may have never been common, even under pristine, pre-grazing conditions. If this is true, the combination of natural scarcity with contemporary grazing or other disturbances may now be jeopardizing the species. As an initial step, *M. evanescens* should be added to federal and state lists of *candidate* endangered species. Although confirmed from Idaho, Oregon, and California, it is expected that northern Nevada is also within the historic range of the species. Placing *M. evanescens* on candidate lists will bring the species to the attention of land managers in these states and will help justify inventory and research, which may in turn ascertain that the species is not particularly rare and has merely been overlooked by collectors. However, until this is established it is prudent to consider the species extremely vulnerable, with ample protection given to any sites occurring on public lands.

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MORPHOLOGICAL AND HOST-SYMBIONT STUDIES OF *TRICHODINA TENUIFORMIS* AND *APIOSOMA CAMPANULATUM* INFESTING MOTTLED SCULPIN (*COTTUS BAIRDI*) FROM PROVO RIVER, UTAH

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ABSTRACT.—*Trichodina tenuiformis* Stein, 1979 and *Apiosoma campanulatum* Timofeev, 1962 were found on gills of mottled sculpin (*Cottus bairdi*) from two locations in the Provo River, UT. They were studied by light and electron optics. Dimensions and morphology of the adhesive disc and denticles of *T. tenuiformis* were differentiated from other *Trichodina* species. *A. campanulatum* was characterized by its spindle-shaped cell body. Fine features examined by scanning electron microscopy included body shape, pellicle, elements of the adhesive disc, aboral ciliary complex, and adoral ciliary spiral. Histopathological studies suggested that the organisms are ectocommensals. Ecological aspects of organism infestation between two areas were also investigated. This report establishes a new host and distribution record for these two species in mottled sculpin from the Provo River, UT.

Key words: Trichodina tenuiformis, Apiosoma campanulatum, Cottus bairdi, *morphology, host-symbiont relationship, ecological aspects, Provo River.*

High numbers of two ciliated protozoa, *Trichodina* and *Apiosoma,* were encountered on the gills of mottled sculpin (*Cottus bairdi*) during a study of ectoparasites of fishes from the Provo River.

Trichodina is a mobile ciliate belonging to the subclass Peritrichia, family Trichodinidae (Lom and Dykova 1992). This protozoan has an adhesive disc characterized by very prominent and taxonomically significant denticles (Van As and Basson 1987). More than 140 species of *Trichodina* have been reported from wild, cultured, and laboratory fishes in many parts of the world (Rand 1993).

Sessile peritrich ciliates of the genus *Apiosoma* (syn. *Glossatella*) belong to the subclass Peritrichia, family Epistylididae (Lom and Dykova 1992). They are generally attached to fish by a scopula (Lom 1973). They have been largely neglected by fish parasitologists until recently, when more attention has been given to this group.

Many species of these two ciliated protozoa have been investigated (Arthur and Margolis 1984, Cone and Odense 1987, Rand 1993); however, a detailed study on mottled sculpin has never been reported. Objectives of this study were to (1) incorporate different levels of microscopy to study ciliate structure, (2) observe histopathological changes these protozoa may cause to the host, and (3) evaluate the seasonal infestation rate to provide ecological information for the listed ciliates and their host.

MATERIALS AND METHODS

Studies were carried out in late summer and fall (August, October 1993), late winter and spring (March, May 1994). Water temperatures in the Provo River ranged from 14°C to 4°C and 6°C to 10°C, respectively. One hundred sixty sculpin were collected from two sites: one in the city of Provo (Utah County) municipal area, the second in a relatively pristine region near the Jordanelle Reservoir (Wasatch County). Sculpin were collected using electrofishing, placed in buckets containing river water, transported to the laboratory, and examined within 24 h after capture.

For light microscopy, air-dried smears of gill filament scrapings were prepared from freshly killed fish and treated by Klein's dry silver impregnation technique (Clark and Heckmann 1984) to examine components of the adhesive disc. Other smears were prepared, fixed, air-dried, and stained with iron hematoxylin (Garcia and Bruckner 1988) to observe the position and structure of the macro- and micronuclei. Sections of infested gills from the spring sample were fixed, blocked, cut, and stained with hematoxylin-eosin (Garcia and Bruckner 1988) for histopathological studies.

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For scanning electron microscopy, gills of freshly killed fish were fixed in 2% buffered glutaraldehyde, followed by repeated washes in a sodium cacodylate buffer and post-fixed in a 1% solution of osmium tetroxide. After that they were washed in the same buffer system. Specimens were dehydrated through a graded alcohol series and critical-point-dried and sputter-coated with gold for examination with a Joel-840 high-resolution scanning electron microscope.

For transmission electron microscopy, after fixation and dehydration, gills were embedded in Spurr resin and sectioned with a glass knife. Each section was stained with lead citrate and examined with a Philip EM400 transmission electron microscope.

Terminology and methods of measurement follow those given by Lom (1958), Lom and Dykova (1992), Wellborn (1967), Arthur and Margolis (1984). Measurements are in micrometers (μm) and are based on 30 specimens for each species from each of the four sampling periods; range is followed by the mean and ± standard deviation in parentheses.

RESULTS

Morphology

Trichodina tenuiformis Stein, 1979

HOST.—*Cottus bairdi* (Pisces: Cottidae).

LOCALITY.—Provo River, Utah and Wasatch counties, Utah.

SITE OF INFESTATION.—Gill filaments.

LIGHT MICROSCOPY.—Body 39–53 (44.2 ± 4.0) dia (diameter). Adhesive disc 19–30 (26.3 ± 2.8) dia, surrounded by a border membrane 2–3 (2.5 ± 0.4) wide, with fine transverse striae. Various-sized light forms present in center of adhesive disc when silver-impregnated. Denticular ring 13.5–20 (17.2 ± 1.8) dia, consisting of 20–26 (23.7 ± 1.3) denticles with 6–10 (7.8 ± 0.8) radial pins per denticle. Denticle with conical central portions 0.7–1 (0.99 ± 0.06) from which a thorn 2.5–4 (2.9 ± 0.4) extends externally with broadly rounded lobes, tapered slightly to a blunt tip and blade 2–3 (2.3 ± 0.3) attached to central region, some with rounded ends (Figs. 1, 2).

Macronucleus horseshoe-shaped 27–48 (39 ± 5.7) dia and approximately 10 μm thick. Micronucleus in -Y position (Lom 1958) observed in six specimens, dimension 3 × 2 (Fig. 3).

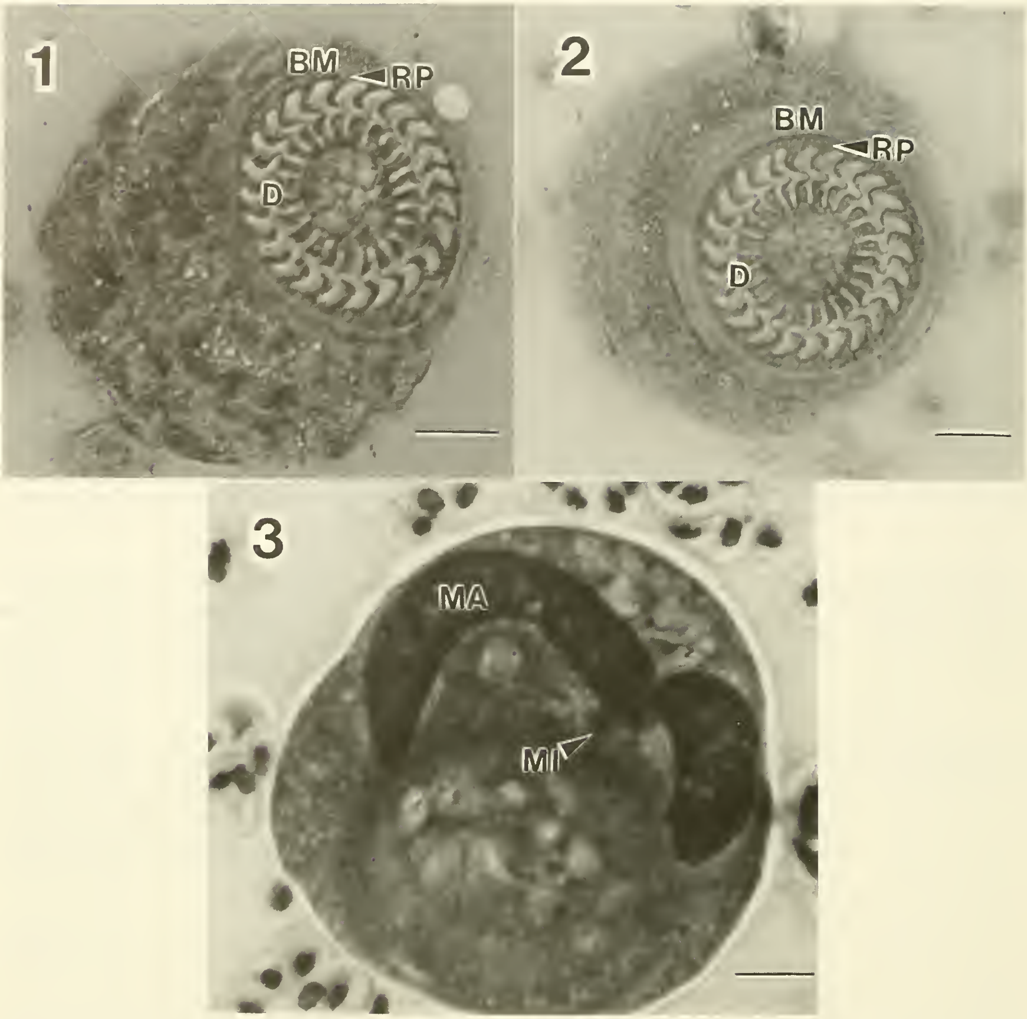
SCANNING ELECTRON MICROSCOPY.—Body of *T. tenuiformis* circular in aboral view and aboral surface relatively flat (Fig. 4). Body bell-shaped or domed when viewed from the side (Fig. 5).

The aboral ciliary complex consists of three distinct ciliary bands: the basal ciliary ring, locomotor ciliary wreath, and marginal ciliary ring. The basal ciliary ring, adjacent to the border membrane, has a single row of fine, distally tapering cilia 1–2 μm long. Separated from the basal ciliary ring by the basal septum is the locomotor ciliary wreath, which is composed of numerous rows of well-developed, powerful cilia 2–3 μm long whose primary function is locomotion. The precise number of ciliary rows composing this wreath could not be ascertained. It is separated anteriorly from the marginal ciliary ring by a poorly developed anterior septum that is evident only when the aboral ciliary complex is uncovered by the velum. The marginal ciliary ring is difficult to distinguish from the locomotor ciliary wreath in *T. tenuiformis.* The velum is a thick, well-developed structure covering the bases of the cilia of the aboral ciliary complex and separating this complex from the adoral ciliary spiral (Figs. 5, 6).

The adhesive disc has a smooth pellicular surface beneath which the outline of the denticles can be clearly seen. The disc is surrounded peripherally by a 2-μm-wide border membrane, which functions to seal the margin of the disc during adherence and contains fine vertical striae over its entire surface. These striae on the internal surface of the border membrane are the radial pins that give the membrane rigidity while retaining its ability to conform to the host's surface (Fig. 7).

The adoral ciliature forms a counterclockwise spiral of about 270°. The base of each cilium is inserted into a deep furrow and hidden from view when SEM is used (Fig. 8).

DEPOSITION OF SLIDES.—One slide (HWML 37721) of silver-impregnated specimens and another slide (HWML 37724) of iron-hematoxylin–stained specimens are deposited in the Harold W. Manter Laboratory, University of Nebraska State Museum. The senior author has additional slides in her collection.



Figs. 1–3. Light micrographs of *Trichodina tenuiformis:* 1–2. Silver-impregnated specimens showing body shape and arrangement of components of the adhesive disc. BM, border membrane; D, denticle; RP, radial pins. Bar = 10 μm. 3. Iron-hematoxylin–stained specimen showing horseshoe-shaped macronucleus (MA); arrow points to the micronucleus (MI). Bar = 10 μm.

Apiosoma campanulatum Timofeev, 1962

HOST.—*Cottus bairdi* (Pisces: Cottidae).

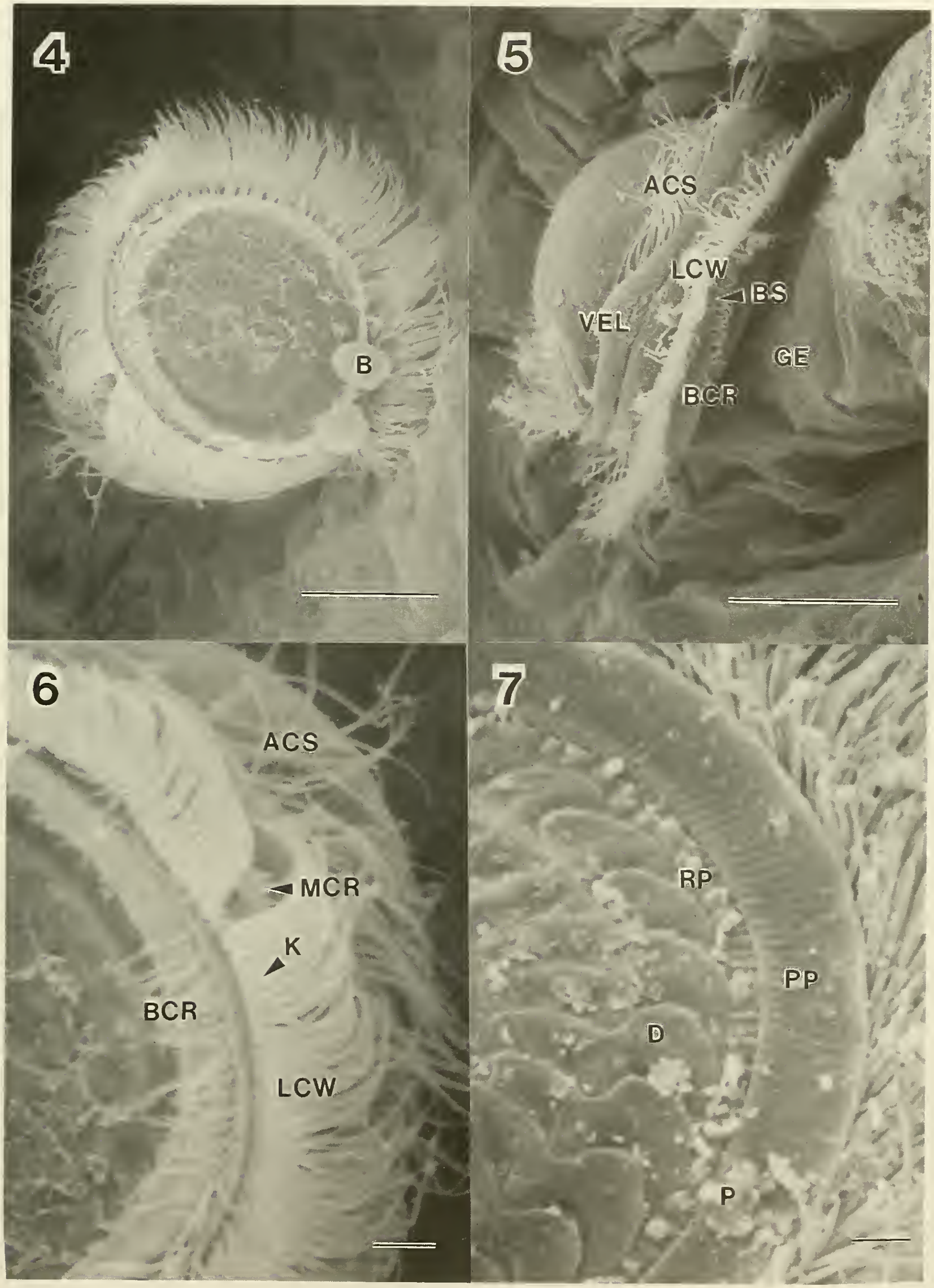
LOCALITY.—Provo River, Utah and Wasatch counties, UT.

SITE OF INFESTATION.— Gill filaments.

LIGHT MICROSCOPY.—Body campanulate. Macronucleus round or slightly conical. Size of stained specimens 31.0–66.0 (47.8 ± 7.2) long by 25.0–45.0 (35.6 ± 4.2) wide. Macronucleus 11.0–20.0 (15.6 ± 2.4). Micronucleus not observed (Fig. 9).

SCANNING ELECTRON MICROSCOPY.—The spindle-shaped body is the characteristic feature of this species. Circular striations of pellicle conspicuous. Pellicle wrinkled into longitudinal furrows. Upper part of body bears the adoral zone, consisting of a tuft of 1–2-μm-long cilia. Most specimens viewed with SEM have contracted peristomes and contracted peristomial lips (Fig. 10).

DEPOSITION OF SLIDES.—A representative slide of *Apiosoma campanulatum* (silver stain) is deposited in the Harold W. Manter Laboratory, University of Nebraska State Museum (HWML 37722). The senior author has additional slides in her collection.



Figs. 4–7. Scanning electron micrographs of the surface of *T. tenuiformis:* 4. Aboral view of entire specimen of *T. tenuiformis.* B, bacteria. Bar = 10 μm. 5. Lateral view of entire specimen of *T. tenuiformis.* ACS, adoral ciliary spiral; BS, basal septum; BCR, basil ciliary ring; GE, gill epithelium; LCW, locomotor ciliary wreath; VEL, velum. Bar = 10 μm. 6. Higher magnification of Figure 4 showing the structure of aboral ciliary complex. ACS, adoral ciliary spiral; BCR, basal ciliary ring; K, kinetosomes; LCW, locomotor ciliary wreath; MCR, marginal ciliary ring. Bar = 1 μm. 7. Adhesive disc of *T. tenuiformis.* D, denticle; PP, peripheral pins; RP, radial pins. Bar = 1 μm.

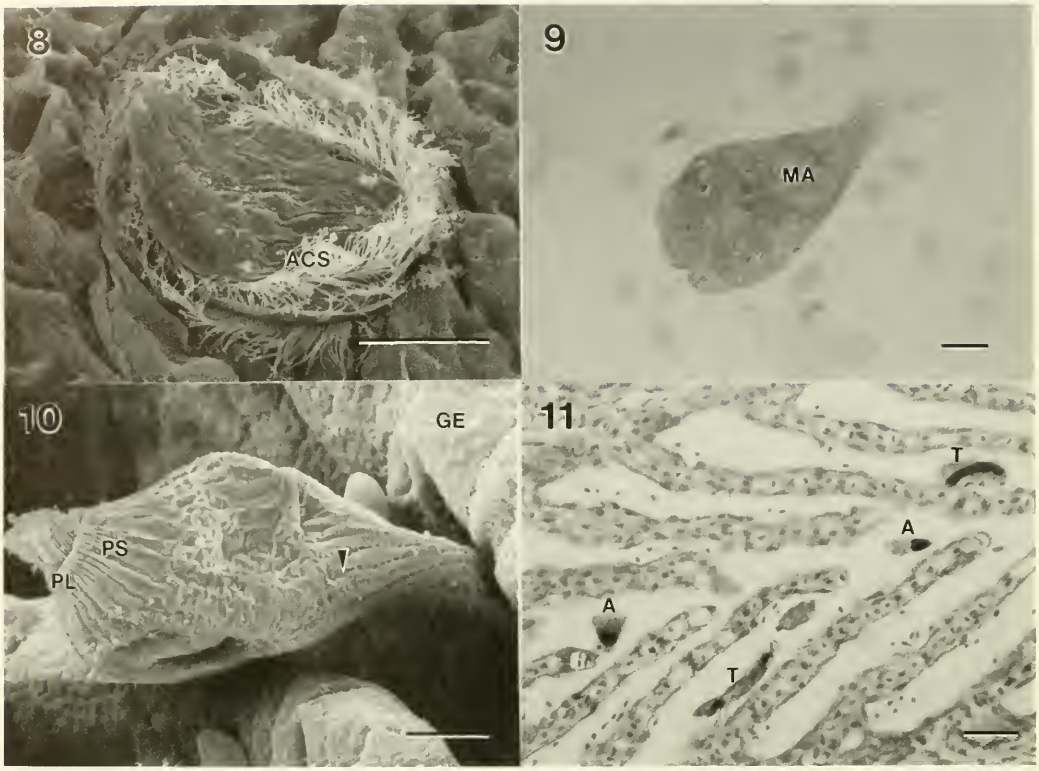


Fig. 8. Adoral view of *T. tenuiformis* showing how the adoral ciliature (ACS) forms a counterclockwise spiral of about 270°. Bar = 10 μm. Fig. 9. Light micrograph of *Apiosoma campanulatum*. Note conicle-shaped body. MA, macronucleus. Bar = 1 μm. Fig. 10. Scanning electron micrograph of *A. campanulatum* attached to the gill epithelium (GE). Note transverse striations of pellicle and its longitudinal furrows (arrow). PL, peristomal lip; PS, peristome. Bar = 5 μm. Fig. 11. Light micrographs showing *Trichodina* (T) and *Apiosoma* (A) infested gill epithelium. Bar = 20 μm.

Host-Symbiont Relationships

Light microscopy.—Sections of mottled sculpin gills had no apparent pathological damage. The conical body of some *A. campanulatum* appeared to be attached to host gill surfaces by the scopula, while others were freely distributed over the epithelial surface. Most *T. tenuiformis* glide over the surface; only a few ciliates adhere to the host epithelial cells (Fig. 11).

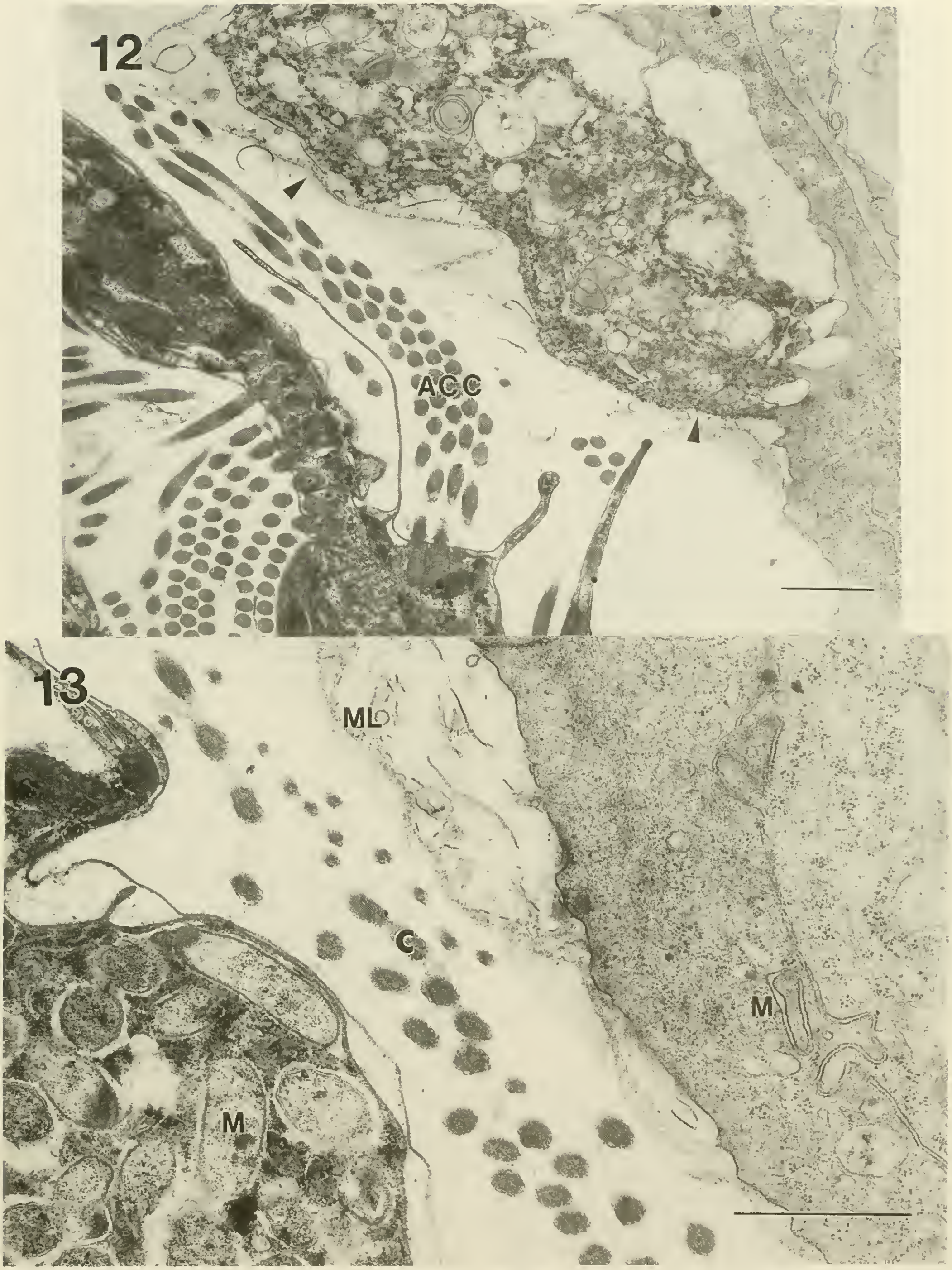
Transmission electron microscopy.—Sections of the interface between the host epithelial cell and *T. tenuiformis* were prepared. No permanent or temporary structure could be detected between the adhesive disc, adoral zone of cilia, and gill epithelial cells (Fig. 12). However, injury to the epithelium due to *T. tenuiformis* can be detected by the number of mitochondria, which decrease and disappear in the immediate host cell. Host necrotic tissue, mucous layers from gill epithelium, and particles dispersed in the water were on the surface of *T. tenuiformis* (Fig. 13).

No ultrastructural damage was observed for *A. campanulatum*. Presence of this ciliate inflicts no serious damage to the host cell. There was some change in number of mitochondria, with cristae showing major changes (Fig. 14).

Ecological Aspects of Infestation

In the Provo River near the Provo residential area, *T. tenuiformis* reached the highest infestation rate in April and May. It was uncommon during summer and autumn and appeared to be absent in the winter. With the increase of water temperature in spring, ciliates reinfested the fish. *Apiosoma campanulatum* at this site maintained an average of 35% infestation rate (no. of infested fish vs. no. of total examined fish) for all seasons.

In the upper Provo River the tendency of infestation of *T. tenuiformis* corresponded closely



Figs. 12–13. Transmission electron micrographs of gill epithelium infested by *T. tenuiformis*. 12. Host necrotic tissue (arrows) sloughs off for parasite's food. ACC, aboral ciliary complex. Bar = 1 μm. 13. Interface between *T. tenuiformis* and mucous layer (ML) of epithelial cells. Note damage to mitochondria (M). C, cilia. Bar = 1 μm.

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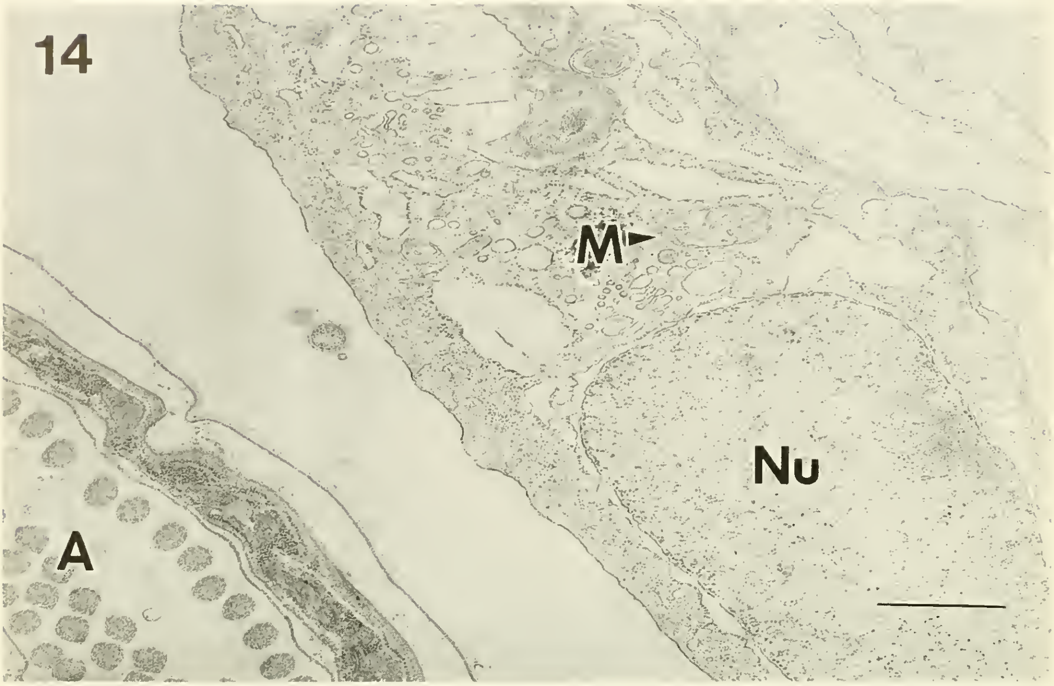

Fig. 14. Transmission electron micrograph of gill epithelium infested by *A. campanulatum*. *A. campanulatum* (A) causes number of mitochondria (M) to decrease and cristae to disappear. M, mitonchondria; Nu, nucleus of epithelial cell. Bar = 1 μm.

to that of the lower area. The highest infestation rate occurred in May and then decreased until the next spring. Percentage of fish infested by *T. tenuiformis* in the lower river area was 20.5% vs. 12.5% in the upper Provo River. Similar to that of the lower river, *A. campanulatum* at the upper site had an average of 37% infestation in all four seasons. In general, *Apiosoma* did not show measurable fluctuations with seasons.

DISCUSSION

Taxonomy and host-symbiont studies of *Trichodina* and *Apiosoma* infesting fishes in the United States have received surprisingly little attention considering the frequency with which these organisms have been associated with fish diseases (Khan et al. 1974, Cone and Odense 1987, Khan 1991). Wellborn (1967) described 13 species of *Trichodina* in southeastern United States, but few reports have been published for this ciliate west of the Mississippi River (Hechmann et al. 1987). Little information is available on *Apiosoma* studies in this country, which is not the case in the former Soviet Union (Bauer 1984). *Cottus bairdi* represents a new host record for *Trichodina tenuiformis* and *Apiosoma campanulatum.*

Comparative Morphology

At the LM level comparison of the adhesive disc of *T. tenuiformis* with that of other species of *Trichodina* reveals a few similarities. *Trichodina reticulata* Hirschmann and Partsch, 1955 described from *Carassius auratus* has denticles similar to *T. tenuiformis* (Bauer 1984). The adhesive disc of the former has a central light zone separated into reticulated structures. But *T. reticulata* differs in having larger overall dimensions (average adhesive disc diameter is 60 μm vs. 25 μm for our material). *T. tenuiformis* has a close affinity to *T. elegans* described by Stein (1979) from fish in Russia. The latter is characterized by an unbroken light zone in the adhesive disc. Our specimens have various-sized light forms in the center of the adhesive disc. To a lesser extent *T. tenuiformis* is similar to *T. puytoraci* Lom, 1962 and *T. domerguei* Dogel, 1940; however, denticle shape and structure of the adhesive disc clearly distinguish *T. tenuiformis* from these species.

Surface features of the adhesive disc and arrangement of the aboral ciliary complex of *T.*

tenuiformis seen by SEM were generally similar to those described for *T. truttae*, an ectoparasite on pacific salmon (*Oncorhynchus* spp.) and steelhead trout (*Oncorhynchus mykiss*; Arthur and Margolis 1984), and *T. labrisomi*, an ectoparasite on hairy blenny (*Labrisomas nuchipinnis*; Rand 1993). However, in *T. tenuiformis*, aboral cilia length is generally shorter than in those previously described. Furthermore, comparison of the aboral ciliature of *T. tenuiformis* with these species of *Trichodina* showed some differences in the extent of development of the anterior and basal septa, in velum structure, and in the degree of evidence of the marginal ciliary ring. The anterior septum is relatively large and the basal one is small in *T. truttae*, whereas in *T. tenuiformis* the basal septum is prominent. The velum is well developed in both *T. labrisomi* and *T. tenuiformis*, but *T. tenuiformis* lacks any protuberances (Rand 1993). Similar to *T. labrisomi*, the marginal ciliary ring of *T. tenuiformis* is poorly developed and cannot be distinguished from the locomotor ciliary ring, whereas in *T. truttae* the marginal ciliary ring is well developed (Arthur and Margolis 1984). Rand (1993) has suggested these marginal ciliature are sensory structures associated with feeding and orientation. Unlike *T. labrisomi* and *T. truttae*, *T. tenuiformis* has no pellicular pores between denticles and the pellicular ridges on the oral surface, which might be a species-specific characteristic for these two species respectively (Arthur and Margolis 1984, Rand 1993).

Over 50 species of *Apiosoma* have been recorded from fishes, the majority of which have been described by Russian authors (Bauer 1984). Although some are common fish parasites in some parts of the world, only one reference concerning *Apiosoma piscicola* on *Salvelinus fontinalis* was reported in North America (Cone and Odense 1987). There is a paucity of data pertaining to *Apiosoma* over the last two decades, likely reflecting taxonomic difficulties due to variability in ciliary structure and lack of strict host-specificity.

Apiosoma conica has a body shape similar to *A. campanulatum*. But our specimens compared more closely to the original description of *A. campanulatum*.

The species identifications were based on original descriptions from Europe; there is a possibility that the two species described in this content are not absolutely identical on both continents.

Host-Symbiont Relationships

Trichodina tenuiformis is an ectocommensal with a tendency to be parasitic in mottled sculpin. There were no visible pathological symptoms with light microscopy; however, electron microscopy disclosed changes in the organelles of host epithelial cells infested by *T. tenuiformis*. Mitochondria decreased in number and disappeared, which might indicate respiratory blockage due to lack of oxygen. This change in mitochondria was observed in *Trichophrya* infesting other fish (Heckmann and Carroll 1985). Necrotic host epithelial tissue sloughs off following organelle loss, supplying sustenance for the parasite.

No serious damage to mottled sculpin could be observed for *A. campanulatum*. Lom (1973) suggested that this simple ectocommensal relationship could change to parasitism in case of heavy invasions, although this tendency is much less pronounced than in trichodinids.

Ecological Aspects of Infestation

This study shows that the infestation of *Trichodina* has both seasonal and regional fluctuations. The higher infestation rate on fish came from the Provo residential area during the spring sampling period. Heavy impact from the local human population may contribute to this infestation. After summer, the number of *T. tenuiformis* gradually reduces with the decrease of water temperature and reaches the highest number the following spring. This may be related to the ciliate life cycle.

Unlike *T. tenuiformis* in this study, *A. campanulatum* maintained a fairly constant infestation on mottled sculpin from the two sites on the Provo River in all four seasons.

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EFFECTS OF HORSE GRAZING IN SPRING ON SURVIVAL, RECRUITMENT, AND WINTER INJURY DAMAGE OF SHRUBS

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ABSTRACT.—The use of domestic grazers to shift the growth advantage toward shrubs is a commonly applied tool on winter ranges managed primarily for big game. Results from horses grazing in spring indicated grazing also benefits shrub survival, seedling recruitment, and reduced winter injury damage on some species of shrubs.

Key words: winter range, range management, mule deer, horses, shrubs, browse, Utah, revegetation, mountain big sagebrush, Douglas rabbitbrush, true mountain mahogany.

On winter ranges managed primarily for big game, the management alternative often selected to maintain the desired mixture of shrubs and understory herbage is grazing by livestock in spring. Numerous studies have reported the benefits of spring livestock grazing to maintain and improve stands of shrubs on winter ranges (Christensen and Johnson 1964, Smith and Doell 1968, Jensen et al. 1972, Hull and Hull 1974, Reiner and Urness 1982, Austin et al. 1994, and others). However, information is limited concerning shrub responses to the effects of livestock grazing with respect to (1) survival of individual mature plants, (2) seedling recruitment, and (3) winter injury damage. In this study the responses of shrubs to domestic horse grazing treatments in spring are reported for *Artemisia tridentata* var. *vaseyana* [Rydb.] Beetle (mountain big sagebrush), *Chrysothamnus viscidiflorus* [Hook.] Nutt. (Douglas rabbitbrush), and *Cercocarpus montanus* Raf. (true mountain mahogany).

METHODS

The study site, located on the foothills east of Logan, UT, 41°46′ N latitude, 111°47′ W longitude, at 1600 m elevation, contained three 50 × 50-m adjoining paddocks. Within each paddock the three browse species were hand-planted from transplants in spring 1983 in 5 × 5 clusters of 25 plants, with 1 m between plant centers. Seven clusters were planted in each paddock, with each cluster separated by a minimum of 20 m. Before planting, all vegetation was removed by root plowing; for two growing seasons following planting, all seedlings were removed by hand and rototiller weeding. Between 1983 and 1987 the three paddocks received equal use by mule deer (*Odocoileus hemionus*) in winter and no livestock grazing. A detailed description of the site is found in Olsen-Rutz and Urness (1987).

This study was conducted during the six growing seasons between spring 1987 and fall 1992. In spring 1987 all shrub seedlings that had become established from seeds were removed from each paddock by hand pulling to minimize soil disturbance. The number of surviving, previously transplanted shrubs within each cluster was counted.

Paddocks were randomly assigned a grazing treatment by horses as heavy, moderate, or protected. Three to seven horses were used, depending upon herbage production, to obtain utilization levels of 35–50% and 65–80% for moderate and heavy treatments, respectively. Horses were selected as grazers because of their high foraging selectivity for grasses and avoidance of shrubs, and the managerial opportunity to manipulate the herbaceous understory to improve shrub growing conditions (Reiner and Urness 1982). Paddocks were grazed yearly between 1 May and 30 June 1987–1991. In 1992 all paddocks were rested from grazing. In the moderately and heavily grazed paddocks, herbage production, comprised almost entirely of annual grasses, and percent utilization were determined from four paired 1-m^2 basketed and unprotected plots, randomly placed in spaces between clusters. Baskets were constructed from 1.2-m-high netting wire supported by steel fence posts. Plots were reestablished and relocated yearly before grazing.

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In fall 1992 all surviving shrubs were counted by cluster, all seedlings within 10 m of each cluster were counted, and percent winter injury damage was visually estimated. Winter injury was defined as the amount of dead stems and twigs as a percentage of total dead plus live stems and twigs. Damage was estimated at five-unit increments from 0 to 95%.

Because we were not able to replicate the three paddocks established for the previous study, we considered clusters as experimental units. We agree with Hurlbert (1984), who described this experimental design as "simple pseudoreplication," but because of constraints of time, space, and costs, this design was the only option. Consequently, we recognize that differences between treatments could be caused by inherent differences between paddocks, but argue that potential spatial error is low due to adjoining paddocks, identical use during the three years preceding our experiment, simple grazing treatments applied, and lack of differences in the number of surviving seedlings among paddocks for each species ($P > .10$) at the beginning of the experiment.

T tests of the means were used to determine differences between grazed and protected plots within and among paddocks. For plant survival a split-plot design using repeated measures (1987 and 1992 data) analysis of variance determined treatment and year effects. One-way ANOVAs assessed differences among treatments for species within years. For seedling recruitment, because all seedlings were removed in 1987, one-way ANOVAs were used for species within years. For winter injury damage, differences between treatments were analyzed using chi-square tests. A significance level of $P < .10$ was used for all tests.

RESULTS AND DISCUSSION

Horse Grazing

Horse use reduced herbage at the end of the grazing period during all years in both the moderately and heavily grazed treatments ($P < .10$), except in 1987 when neither treatment was different from protected plots. Mean herbage utilization during all years was 46% in the moderately grazed treatment and 71% in the heavily grazed treatment. Following grazing, remaining herbage was different between the moderately and heavily grazed treatments during all years except 1987. Herbage production in protected plots was not different from the moderately and heavily grazed treatments during the first three years. However, the heavily grazed treatment had lower production during the last two years, suggesting that heavy grazing by horses reduced production of herbage.

Shrub Survival

Horse grazing increased survival of *Artemisia* ($P = .01$) and *Cercocarpus* ($P = .10$) but had no effect on *Chrysothamnus* (Table 1). All three species declined in numbers between 1987 and 1992 ($P = .001$).

In 1987 the number of surviving plants among treatments for *Artemisia*, *Chrysothamnus*, and *Cercocarpus* was not different (Table 1). However, in 1992 the number of surviving *Artemisia* plants among treatments was different ($P = .005$). The protected treatment had lower survival than both the moderately and heavily grazed treatments ($P = .001$), but the moderately and heavily grazed treatments were not different. Similarly, for *Cercocarpus* the number of surviving plants among treatments was different ($P = .03$). The protected treatment had lower survival than both the heavily ($P = .005$) and moderately ($P = .10$) grazed treatments, but the moderately and heavily grazed treatments were not different. For *Chrysothamnus*, no differences were found.

Seedling Recruitment

For *Artemisia*, seedling recruitment was significantly different among treatments ($P = .08$). The heavily grazed treatment had more seedlings than the protected and moderately grazed treatments ($P = .05$). No differences among treatments were found for *Chrysothamnus*, and no seedlings were counted for *Cercocarpus* (Table 1).

Although the low numbers of seedlings counted in this study require interpretive caution, results are consistent with other studies in which livestock grazing was reported to increase shrub density (Stewart 1941, Christensen and Johnson 1964, Hull and Hull 1974). Furthermore, the results from this study, that horse grazing in spring resulted in higher survival of mature plants and increased seedling establishment for several species of shrubs, are consistent with reports of increased production of shrubs following livestock grazing

TABLE 1. Plant survival (total number/paddock), seedling recruitment (total number/paddock), and winter injury damage (mean % per shrub) of *Artemisia tridentata* (ARTR), *Chrysothamnus viscidiflorus* (CHVI), and *Cercocarpus montanus* (CEMO), as affected by heavy (H), moderate (M), and protected (P) horse grazing treatments[1].

			Year	
	Species	Treatment	1987	1992
Shrub survival			Number/paddock	
	ARTR	H	119	91^{a}
		M	128	93^{a}
		P	120	42^{b}
	CHVI	H	125	110
		M	86	78
		P	106	101
	CEMO	H	164	158^{a}
		M	161	140^{ab}
		P	168	119^{b}
Seedling recruitment[2]			Number/paddock	
	ARTR	H	—	18^{a}
		M	—	5^{b}
		P	—	5^{b}
	CHVI	H	—	2
		M	—	2
		P	—	3
Winter injury damage[3]			Mean % per shrub	
	CEMO	H	—	11^{a}
		M	—	24^{b}
		P	—	41^{c}

[1] Data with different superscripted, lowercase letters within year and species were different at $P < .05$.

[2] No seedlings of CEMO were found.

[3] No winter injury damage on ARTR or CHVI was found.

with horses (Reiner and Urness 1982, Austin et al. 1994), sheep (Jensen et al. 1972), cattle (Smith and Doell 1968), or goats (Riggs and Urness 1989).

Winter Injury

Winter injury was not found on either *Artemisia* or *Chrysothamnus* (Table 1). For *Cercocarpus,* winter injury among treatments was different ($P = .001$), with highest damage occurring on the protected treatment, medium on the moderately grazed treatment, and lowest damage on the heavily grazed treatment. All treatments were different from each other ($P = .001$).

Winter injury has been reported for many shrub species, including *Cercocarpus* (Nelson and Tiernan 1983). However, only one known report compared winter injury to grazing. Contrary to our results, Jensen and Urness (1979) compared heavy (70%) and moderate (35%) levels of grazing of grasses and forbs by sheep and reported that injury to *Purshia tridentata* (antelope bitterbrush) was independent of grazing intensity or time of use.

SUMMARY

Our results support the use of grazing by horses of herbaceous understory in spring to maintain and improve stands of browse for winter use by big game. Herbage production was reduced by heavy grazing, survival of mature plants of *Artemisia* and *Cercocarpus* was increased, recruitment of *Artemisia* was increased, and winter injury to *Cercocarpus* was decreased. No negative effects on shrubs from grazing by horses were found.

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NORTH AMERICAN TYPES OF *OXYTROPIS* DC. (LEGUMINOSAE) AT THE NATURAL HISTORY MUSEUM AND ROYAL BOTANIC GARDEN, ENGLAND, WITH NOMENCLATURAL COMMENTS AND A NEW VARIETY

S. L. Welsh[1]

ABSTRACT.—Specimens of *Oxytropis* in the herbaria of The Natural History Museum and Royal Botanic Garden were examined to interpret their role in nomenclature. This is the first attempt at a systematic overview of specimens so important in understanding the genus as it occurs in North America. The review of specimens at BM and K during the present research has resulted in realignment of names of some of the taxa. *Oxytropis campestris* var. *gracilis* (A. Nelson) Barneby is recognized herein as being predated by *O. campestris* var. *spicata* Hook., *O. sericea* var. *spicata* (Hook.) Barneby is replaced by ***O. sericea*** **var. *speciosa* (Torr. & A. Gray) Welsh comb. nov.**, and *O. campestris* var. *terrae-novae* (Fern.) Barneby is superseded by ***O. campestris*** **var. *minor* (Hook.) Welsh comb. nov.** One new taxon is proposed: ***Oxytropis deflexa*** **(Pall.) DC. var. *pulcherrima* Welsh & A. Huber, var. nov.** Lectotypes are designated for the following taxa: *Astragalus retroflexus* Pall., *Oxytropis arctica* R. Br., *O. arctica* var. α *subumbellata* Hook., *O. arctica* var. β *uniflora* Hook., *O. campestris* var. β *speciosa* Torr. & A. Gray, *O. campestris* var. ξ *melanocephala* Hook., *O. campestris* var. δ *spicata* Hook., *O. multiceps* var. *minor* A. Gray, *O. splendens* Douglas ex Hook., *O. splendens* β *richardsonii* Hook., *O. uralensis* β *subsucculenta* Hook., and *O. uralensis* γ *minor* Hook.

Key words: Leguminosae, Oxytropis, *nomenclature, Natural History Museum, Royal Botanic Garden.*

Concepts of species within a genus undergo an evolutionary progression through time as additional information is obtained. A review of the history of botanical treatments of the genus *Oxytropis* parallels that of other genera in North America, wherein the early explorations, researches, and publications were undertaken by explorers and scientists from the Old World, especially from England. Specimens arriving from the New World were compared to those of the same genera from Eurasia. Specimens of *Oxytropis* from Russia and other regions with arctic, subarctic, or boreal floras arrived piecemeal at herbaria in Europe, where important collections accumulated, particularly at the Royal Botanical Garden at Kew (K) and the Natural History Museum (BM; formerly the British Museum [Natural History]) in London. These materials formed the basis for comparison with North American specimens. Some American plants were similar and were given the same names as some Old World species. The earliest revision of *Oxytropis* based on North American specimens was that of William Jackson Hooker (1785–1865), whose concepts of species, set forth in the *Flora boreali-americana* (Hooker 1831), were to have a profound effect on all later interpretations of the genus. Annotations of the specimens at K and BM present a history of the use of epithets by various botanists interested in this fascinating genus. However, of the revisionary workers on North American members of the genus *Oxytropis*, only Asa Gray appears to have systematically studied the historical collections at the Royal Botanical Garden, Kew, and no one has examined all materials of the genus in North America at the Natural History Museum. Various workers on regional floras, M. L. Fernald, A. E. Porsild, and N. Polunin, have annotated part of the specimens, and R. C. Barneby, whose revision (1952) is a classic presentation of the genus in North America, has examined selected material.

The purposes of this paper are to clarify the status of historical specimens, to record their place of deposit, and to trace their nomenclatural history as it affects interpretation of the genus in North America. Plants at BM and at K are the center of focus for this treatment. However, the location of duplicate types in various herbaria in the United States is also included where that information is known. Names and synonyms of the North American taxa were reviewed previously by Welsh (1991). Abbreviations of the repositories follow Holmgren et al. (1990).

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The synopsis of *Oxytropis* in *Flora boreali-americana* (hereinafter *Flora*) by Hooker is relevant to an understanding of many of the names in the following list. This is true even though Hooker had not seen the materials in the field, and even though his concepts were based on limited and often inadequate materials for a definitive understanding of the taxa. The *Flora* has no introduction outlining the scope and rationale for the treatment. It does, however, contain a very detailed title page:

> Flora Boreali-Americana; or, the Botany of the Northern Parts of British America: compiled principally from the plants collected by Dr Richardson & Mr Drummond on the late northern expeditions, under command of Captain Sir John Franklin, R.N. to which are added (by permission of the Horticultural Society of London,) those of Mr Douglas, from North-West America, and of other Naturalists.

That Hooker does not mention the collections of Captain William Edward Parry and his associates is not to be considered an oversight; their materials had been published previously by Hooker (1825), and their specimens are by no means neglected in the *Flora*. It is unfortunate that the specimens on which the names were based were not routinely so noted by the authors.

The dedication in the *Flora* by Hooker honors both Franklin and Richardson,

> under whose auspices, as Commander and Naturalist of two separate expeditions to The Polar Seas, a great portion of the more rare and interesting plants that ornament this volume were collected, under circumstances of singular difficulty, hardship, and danger.

In this important pioneer work, Hooker recognized only 10 species of *Oxytropis* but regarded several of them as consisting of variants designated by Greek letters, some of which were followed by epithets. The names in order of their appearance are *O. borealis; O. Uralensis* α, β *subsucculenta*, γ *minor; O. arctica* α, β *minor*, δ *inflata; O. foliolosa; O. argentata; O. lambertii; O. nigrescens; O. campestris* α, γ *sulphurea*, δ *spicata*, ε *glabrata*, and ξ *melanocephala; O. splendens* α *vestita* and β *richardsonii;* and *O. deflexa*. These names have occurred in subsequent literature and have been accounted for by various workers of the genus, often without citation of type material or place of deposition. An attempt is made here to associate all names noted by Hooker with their 20th-century equivalents. Hooker's personal herbarium, containing many of the *Oxytropis* types, is at Royal Botanic Garden (K Hooker); those of Richardson, Douglas, Drummond, and Parry and his associates are represented in some part at both K and BM.

Richardson (1823) cited species of *Oxytropis* based on his own findings, but he did not name any as new. The species treated by him include *O. oxyphylla, O. deflexa, O. campestris, O. argentata*, and *O. uralensis*. Of these, only *O. deflexa* stands almost in the same sense today.

The treatment of *Oxytropis* by Torrey and Gray (1838) followed Hooker's account in nearly all details, but it added six new species collected and described by Thomas Nuttall (1786–1859) on his journey across the continent with Wyeth in 1834. These were the first American species described by a botanist who had seen them in the field. The diversity of the species in the American West must have seemed overwhelming even to Nuttall, who proposed several additional species of *Oxytropis* not published in Torrey and Gray's monumental work. Specimens in Nuttall's personal herbarium, which is deposited at BM, are evidence of his belief in a greater number of species than would be published subsequently. Some of the Nuttall names were later cited as synonyms, but some were not mentioned at all. Nuttall was unfamiliar with most members of the genus in the Old World, and some of his proposals reflect that lack of understanding. The difficulty in comprehending a genus as large and complex as *Oxytropis* is understandable and is not confined to the 19th century.

Asa Gray (1810–1888) became the most important 19th-century North American devotee to the genus, revising it twice, once in 1863 and again in 1884. Concepts in the revision of *Oxytropis* by Gray (1884) were influenced by his examination in 1880 of specimens at Kew, which had formed the basis of the treatment by Hooker in the *Flora*, and from the large number of specimens in eastern American herbaria collected during the intervening several decades. Gray's 1884 publication included plants from a broader geographic area than those examined by Hooker and contained descriptions of 16 species. Specimens collected by Nuttall, especially, and several other western American explorers formed the basis of additional species not included in his and Hooker's earlier works. Gray accounted for some proposals, bringing the concepts of the genus to date as new materials had accrued. He accounted for some but not all taxa treated by Hooker, e.g., *O. borealis* DC. under *O. leucantha* (Pall.) Pers. The name *O. leucantha* (Pall.) Pers. was long considered a potential replacement for viscid members of the genus in North America. The type was examined by Welsh (1977) and the name excluded from interpretation of North American taxa. It is a portion of the *O. campestris* complex in Siberia. Most of the other names treated by Hooker were ignored by Gray, cited in synonymy, or provisionally included in other entities. Apparently Gray did not see all pertinent historical material in England, particularly not that at BM. It is evident, likewise, that not all ambiguities are resolved by the research leading to this paper. Nevertheless, as noted by Barneby (1952), "the resulting synopsis of the genus [by Gray] in 1884 stands as a small but enduring monument to his genius."

Barneby (1952), in a classic account, recognized 22 species and 21 additional infraspecific entities as occurring in North America. He accounted for all names used previously in North America, with problematical names being discussed in a list of excluded and imperfectly known species.

A summary treatment of the genus by Welsh (1994) for the Flora North America project likewise treats 22 species, somewhat realigned from those of Barneby, but recognizes 35 infraspecific taxa. Many names proposed at infraspecific rank are from Arctic regions of the continent, areas whose collections were not well represented in herbaria prior to 1950.

Students of plant taxonomy must examine authentic materials of all previously named taxa, whether currently recognized or not. In the 19th century David Douglas (1798–1834), Thomas Drummond (ca 1780–1835), Thomas Nuttall, and Sir John Richardson (1787–1865) were the most important contributors of specimens on which North American names in *Oxytropis* are based. Repositories for their specimens, later designated as types, are Philadelphia Academy of Sciences (PH), New York Botanical Garden (NY), and Gray Herbarium (GH) in the United States, and Royal Botanic Garden at Kew (K) and Natural History Museum (BM) in England. Later in the 19th century several other workers gathered specimens that were considered new to science; these were deposited in numerous other herbaria in addition to those cited above.

David Douglas was an intrepid Scottish botanical explorer of North America whose contributions to *Oxytropis* came from his journey across the continent mainly in 1826–27. He collected the specimens on which the concept of *O. splendens* was based. According to Stafleu and Cowan (1976), the first set of his North American plants is at K; his own herbarium is partly at BM and partly at CGE. Hooker based his treatment of *Oxytropis* in the *Flora* in part on collections by Douglas (Stafleu and Cowan 1979), as evidenced by specimens at K.

Sir John Richardson, British (Scottish) explorer and naturalist with the Royal Navy, was a medical doctor who accompanied Sir John Franklin on two expeditions, 1819–22 and 1825–27, and later (1848–49) commanded an expedition in search of Franklin who was lost on an ill-fated sea voyage of 1845–47 in search of the Northwest Passage. Richardson's herbarium of vascular plants is mainly at BM, with further material at K and elsewhere (Stafleu and Cowan 1983). The first expedition, in 1819–22, was from Great Slave Lake to the Coppermine River, down which they traveled to Coronation Gulf, and then cross-country to the Coppermine in winter of 1821–22. Only 9 of 21 on the expedition survived the ordeals of hunger, cold, and exposure; that anyone survived is a tribute to persistence of the men and aid of local aborigines who rescued them from certain death (Houston 1984). The expedition is remembered as one of the most deadly in the history of biological investigations in North America. Both Richardson and Franklin barely escaped with their lives. The second expedition was down the Mackenzie River to the Polar Sea, with Franklin exploring westward and Richardson eastward along the coast to Coronation Gulf and return. The many plant and animal names proposed by Richardson, and those named after him, serve as a tribute to the genius and perseverance of this remarkable man.

Edward Sabine (1788–1883), John Edwards, James Clark Ross (1800–1862), William Edward Parry (1790–1855), Alexander Fisher, and Charles James Beverley collected plants on the first Parry journey in search of the Northwest Passage (Parry 1821). It is evident from the introduction to Brown's (1824) treatment that each of those named, mainly medical doctors with various ships, made their own collections, which were placed initially in their private herbaria. Sabine was astronomer to the Arctic expeditions led by Parry and collected plants in Melville Island and Greenland. Edwards was surgeon to the *Hecla* on Parry's voyages of 1819, 1820, 1821–23, and Fisher was assistant surgeon on the *Hecla* in the 1819–20 voyage, while Beverley was assistant surgeon on the *Gripper*. Ross was in the Royal Navy with the Parry expeditions in 1819–20, 1821–23, 1824–25, and 1827. Parry was a British explorer who commanded expeditions to the Arctic in search of the Northwest Passage. Specimens from the Parry expeditions are deposited at both K and BM, with some of the collectors' private herbaria better represented at BM and some at K.

Peter Simon Pallas (1741–1811), important for his exploration of Russia and his work on the Russian flora, named *Astragalus deflexus* and *Astragalus retroflexus,* later included in *Oxytropis,* names whose interpretations bear on North American species of the genus. According to Stafleu and Cowan (1983) the main personal herbarium of Pallas was sold at a London auction in 1808 to A. B. Lambert, who subsequently sold one part to Robert Brown and another to William Robertson. Both parts presently are at BM and are pertinent to this paper; additional parts reside elsewhere, but they are not the basis of this treatment except for an important set at LE, which evidently contains the type specimen of *Astragalus deflexus,* which has not been examined for this treatment.

The author wishes to thank the curators at BM and K for their cooperation in providing specimens on loan, and for their hospitality during a visit to London. Also acknowledged is Dr. Rupert Barneby, who read critical portions of the manuscript and who provided suggestions and encouragement.

1. *Aragallus abbreviatus* Greene, Proc. Biol. Soc. Wash. 18: 12. 1905.

= *Oxytropis lambertii* Pursh var. *articulata* (Greene) Barneby

Type: "Texas, near Dallas, Limestone prairie, Dallas County, J. Reverchon 603, May 1876"; holotype NDG!; isotypes NY!, BM!; "Dry calcareous soil near Dallas, Texas. Curtis 603, April, May"; paratype GH!, NDG!, NY!

2. *Aragallus aven-nelsonii* Lunell, Bull. Leeds Herb. 2: 6. 1908.

= *Oxytropis lambertii* Pursh var. *lambertii*

Type: North Dakota, "Aragallus Aven-Nelsoni Lunell, n. sp. Butte, Benson County, N. Dak., June 14, 21, July 2,1908," legit J. Lunell; holotype MIN?; isotypes BM!, NDA!, MIN!, NY!, US!, WTC!

3. *Aragallus invenustus* Greene, Proc. Biol. Soc. Wash., 18: 12. 1905.

= *Oxytropis sericea* Nutt. var. *sericea*

Type: "South Dakota, about Fort Meade, Meade County, W. H. Forwood 96a, 96b, 3 June 1887, 96b, 7 June 1887"; syntypes US!, photo BRY!, K Hooker!

4. *Aragallus majusculus* Greene, Proc. Biol. Soc. Wash., 18: 12. 1905.

= *Oxytropis sericea* Nutt. var. *sericea*

Type: Utah, Henry Mts., Garfield County, Utah, M. E. Jones 5674, July 1894; holotype US!; isotypes NY!, MO!, BM!, photo BRY!

5. *Aragallus metcalfei* Greene, Proc. Biol. Soc. Wash., 18: 12. 1905.

= *Oxytropis lambertii* Pursh var. *bigelovii* A. Gray

Type: New Mexico, Sawyer's Peak, Grant County, open glade, ca 10,000 ft, O. B. Metcalf 1079, 7 July 1904; holotype US!; isotypes NY!, CAS!, GH!, POM, WTC, BM!

6. *Astragalus deflexus* Pall., Acta Acad. Sci. Imp. Petrop. 2: 268. 1779.

= *Oxytropis deflexa* (Pall.) DC. var. *deflexa*

Type: "ad nivalia Dauriae . . . circa Balyra rivum aliosque Ononem influentibus" [Siberia], P. S. Pallas s.n.; holotype LE.

7. *Astragalus retroflexus* Pall., Sp. Astragal., 33, tab. 27. 1801.

= *Oxytropis deflexa* var. *deflexa*

Original location: Provenit haec species tantum in alpinis transbaicalensibus et circa lacum Baical, praesertim in scaturiginosis frigidus, circa fontes rivulorum Baltschikan, Carol, Bargusin et Chilik; verosimillime quoque per omnem alpestrem tractum, Sibiriam a Sinarum Imperio diffinientem.

Type: Pallas, s.n.; lectotype (here selected) BM (#45444)!

There are two Pallas collections labeled *Astragalus deflexus* at BM, 45443 and 45444; the former (paratype) with three stems bears juvenile to mature fruit and a label in Russian script, the latter (lectotype) with a complete plant in flower and two racemes (one in flower and one in immature fruit). Appearing on the sheet with the BM number 45444 on the label are "No. 10" and illegible script. Both collections simulate what has passed in North America as *O. deflexa* var. *sericea* Torr. & A. Gray. Sheet 45444, here designated as lectotype for *Astragalus retroflexus* Pall., is a close match for the illustration in Table 27 of Pallas' Species Astragalorum (1800–1803), except that the drawing is a mirror image of the actual specimen. The reversal of the image comes from the use of the copper plate on which the original drawing was produced. Flower buds, leaves, and leaflets are the same. Only the flowers and their proportions are slightly different; those of the drawing are much too distinct and perhaps too large. The fruiting branch represented in Table 27 is from sheet 45443, again in reverse image, and taken from the branch at the upper left. Pallas (1800–1803) notes that the plant was grown in a garden at St. Petersburg and flowered and produced fruit the second year. It seems that one specimen or both cited above are from plants grown in the garden at St. Petersburg.

8. *Oxytropis argentata* sensu Richardson, Frankl. 1st Jour., Bot. Append. 745. 1823.

= *O. sericea* var. *speciosa* (Torr. & A. Gray) Welsh, pro parte

Authentic specimen: "British North America. Dr. Richardson 1819–22. Astr. argentatus Pallas Astr. Carlton" (BM #45476!).

9. *Oxytropis arctica* R. Br., Chloris Melvill. 20. 1823.

Type locality: Canada, "Melville Island, Parry's First Voyage, Sabine, Edwards, Ross, and others, 1819–1820" (R. Brown l.c.).

Type: "Melville Island, coll. by Mr. Beverley"; lectotype (here selected) K Hooker!; probable isolectotypes S!, GH!

The reverse of the Beverley sheet contains the notations, "Winter Harbour, 23 July 1820 [flowering material?]" and "Winter Harbour, 4th July 1820 [fruiting specimen?, the portion here selected as lectotype]." The Beverley material is the most complete for the species of any of those collected by the Parry expedition members and includes both flowering and fruiting material; the Sabine paratype cited below also has a flowering and a fruiting branch.

Brown (1823) did not designate any specimens to support his new species. However, in the introduction to his list of plants collected in Melville Island, he lists the herbaria of the officers of the expedition on which the list was based. Included are "Captain Sabine, Mr. Edwards, Mr. James Ross, Captain Parry, Mr. Fisher, and Mr. Beverley, whose names are here given in order of the extent of their collections."

The following are paratypes of *Oxytropis arctica* at BM and K: "36. Oxytropis arctica. [illegible]. Melville Id. Mr. James Ross" (BM!); "Parry's First Voyage 1819–20. Melville Island. 11th August 1820, (BM!)"; "Melville Id. Capt. Parry. 36. Oxytropis arctica" (45446 BM!); "Melville Isld., Sabine" (K Hooker!); and "Oxytropis arctica. Mr. Edwards" (BM!).

The literature citation for *O. arctica* has traditionally been given as "Parry's First Voy., Append. 9: 278. 1824." The list of plants by Robert Brown was published twice, however, once as "Chloris melvilliana," in 1823 and subsequently in the appendix to Parry's first voyage. Evidently, Chloris melvilliana was published a year prior to the appearance of identical material under different pagination in the Parry appendix. On an introductory page in Chloris melvilliana is written the following: "The following List is printed as Nl. XI of the Appendix to Captain Parry's Journal of the First Voyage, commencing at page cclix." It is evident that at least page proofs of the Appendix were available at the time the Chloris was ready for printing, and that they formed the basis of the Chloris.

9a. *Oxytropis arctica* var. *subumbellata* Hook. in W. E. Parry, Sec. Voy. 4: 396. 1825.

= *O. nigrescens* var. *nigrescens*

Type locality: "Arctic shores and Islands of North America. Capt. Sir E. Parry; Dr. Richardson; Capt. Sir John Franklin; Capt. Back, & c." (Hooker 1831: 146).

Type: "Dr. Richardson. 1/146. Oxytropis arctica Br. var. subumbellata. Coast"; lectotype (here selected) BM!

The lectotype at BM consists of four specimens of *Oxytropis nigrescens* var. *nigrescens*, and they are mounted on one sheet with four specimens of *O. nigrescens* var. *uniflora* bearing the label, "Oxytropis arctica β, Frankl. Exp. Dr. Richardson."

9b. *Oxytropis arctica* var. *uniflora* Hook. in W. E. Parry, Append. Parry Sec. Voy. 4: 396. 1825.

= *O. nigrescens* (Pall.) Fischer var. *uniflora* (Hook.) Barneby

Type: "Barrow River, E coast Melville Peninsula, lat. 67°21'N, on Parry's Second Voyage, Edwards s.n. 1821–3"; lectotype (here selected) BM!; isolectotypes K Hooker!, GH!, NY!

The Barrow River lectotype at BM, a mere fragment with three flowers, is mounted with a second much more complete collection, "Igloolik. Mr. Edwards, Parry's 2nd Voyage" (a paratype). The collection from Igloolik consists of several flowering specimens and one with a solitary fruit. Additionally, there are four almost mature fruits, two of which have been opened displaying the septum. There are several sheets of this variety at BM taken on various Parry voyages (e.g., BM 45452, "Oxytropis arctica, Barrow River, 1822"). The isolectotype at K Hooker is similarly a mere fragment.

9c. *Oxytropis arctica* δ *inflata* Hook., Fl. Bor.-Amer. 1: 146. 1831.

= *O. podocarpa* A. Gray

Type: "Highest summits of the Rocky Mts. Drummond"; holotype K Hooker!

The Drummond material at K consists of six plants, one of which is in young fruit; they are mounted with two specimens by Beechey from Kotzebue Sound, both of which appear to be *O. nigrescens*. Gray cited the Drummond material with several other specimens when he described *O. podocarpa* (q.v.).

9d. *Oxytropis arctica*, "*varietas notabilis*," R. Br., Chlor. Melvill. 51. 1823.

= *O. nigrescens* (Pall.) Fischer var. *uniflora* (Hook.) Barneby

The name as noted above was cited by Barneby (1952) as not validly published; it is here included for consistency of use in North American literature on the genus *Oxytropis*. Hooker (1825), in the botanical appendix to Parry's Journal of a Second Voyage, notes in his discussion of *O. arctica:*

> This variety (β.) is noticed by Mr. Brown at the end of his valuable *Remarks on the Flora of Melville Island*, as discovered by the gentlemen of the present expedition, and says of it, "Varietas notabilis, vix enim distincta videtur species, statura minor, scapo unifloro passemque umbella biflora, dentibus calycis respecti tubi paulo longioribus, foliolis saepe 7, quandoque 7, villis persistentibus utrinque argento-sericeis." . . . To these remarks I may add, that the plants are not above half the size of α [*subumbellata*], the stems less woolly, the leaflets fewer, denser, and cov-

> ered with short, very white silky hairs. The peduncle scarcely rises above the leaves, and each subtended by small bractea. The corolla is of the most beautiful deep purplish blue; the calyx and legume black from the quantity of black hairs; but these are mixed with several longer white ones. The contrast between the deep blue of the corolla and the dense, white and silvery leaves render this a most lovely little plant.

The specimens are still silvery white and beautiful after more than 17 decades.

10a. *Oxytropis arctobia* Bunge, Mem. Acad. Imp. Sci. Saint-Petersbourg 22: 114. 1874.

= *O. nigrescens* (Pall.) Fisch. var. *uniflora* (Hook.) Barneby

Type: "Habitat in arcticis Americae borealis; v. s. sp. in herb. olim Fischerano nunc h. bot. Petrop." (Bunge l.c.).

This was based by Bunge (1874) exactly on a specimen of *O. arctica* β *uniflora* Hook., in the Fischer herbarium at LE. The name was utilized by some (Polunin 1940) for North American specimens.

10b. var. *hyperarctica* Polunin, Bot. Canad. E. Arctic, 293. 1940.

= *O. nigrescens* (Pall.) Fisch. var. *uniflora* (Hook.) Barneby

Type: "Franklin district, Baffin Island, Arctic Bay, N. Polunin 2583, 8–11 Sept. 1936"; holotype CAN; isotypes GH!, BM!, OXF!

11. *Oxytropis borealis* DC. Prodr. 2: 275. 1925.

It appears that the name was not used by Hooker in the modern sense as interpreted by Welsh (1990). The name appears on a sheet of *O. maydelliana* Trautv. in the Hooker herbarium at K. It is, however, the earliest name available at species rank for the viscid-glandular material that has passed under *O. viscida* Nutt., and other taxa (see various uses elsewhere in this paper).

12a. *Oxytropis campestris* (L.) DC. var. *davisii* Welsh, Leafl. W. Bot. 10: 25. 1963.

Type: "British Columbia, mi 403.4, Alaska Hwy, R. J. Davis 6076, 19 July 1962"; holotype BRY!; isotype IDS!

Distribution: SW Alberta, NE British Columbia.

This taxon has been represented in herbaria since early in the 19th century. Specimens by Douglas and Drummond, almost assuredly assignable to this taxon, are present at BM and K. Their collections formed portions of the concepts *O. lambertii* β. Hook. (q.v.) and *O. uralensis* γ *minor* Hook. (q.v).

This plant is readily distinguished by its colorful flowers, fasciculate leaflets or tendency to fasciculate leaflets, and elongate inflorescences. Specimens have been considered as intermediates between members of the *Oxytropis campestris* complex and *O. borealis* var. *viscida*, or they have been misidentified as *O. splendens* because of the fasciculate leaflets. Plants of var. *davisii* are locally abundant on stream gravels and adjacent slopes in the foothills mainly of the Alberta Rockies and in northeastern British Columbia. Intermediates between var. *davisii* and *O. sericea* var. *speciosa* occur in northern British Columbia. Another variety with pink-purple flowers, var. *roaldii* (Lindstr.) Welsh, occurs in northern Yukon Territory and adjacent Alaska. The northern plant is of low growth and has fewer flowers than var. *davisii*. A similar pair of low versus tall varieties, partially sympatric, exists in eastern Canada, i.e., var. *johannensis* Fernald and var. *minor* (Hook.) Welsh [var. *terrae-novae* (Fernald) Barneby].

12b. *Oxytropis campestris* ε *glabrata* Hook., Fl. Bor.-Amer. 1: 147. 1831.

= *O. maydelliana* Trautv.

Type locality: "Bear Lake to the Arctic Shores and Islands, Dr. Richardson; Capt. Sir J. Franklin and Capt. Back; Capt Sir E. Parry, &c." (Hooker l.c.).

Type: Bear Lake to the Arctic Shores and Islands; neotype GH!

Hooker characterized the taxon "foliolis glabriusculus subsucculentis." No authentic material of var. *glabrata* was discovered at either K or BM.

Hooker's statement of the locality information applied to both vars. *glabrata* and *melanocephala*. The specimen at GH, annotated by Gray indicating that it was based on Hooker's var. *glabrata*, is here designated as neotype. Thus, the name is fixed in the sense used by Barneby (1952).

12c. *Oxytropis campestris* var. *johannensis* Fernald, Rhodora 1: 88. 1899.

Type: "Maine, gravelly shores, valley of St. John River, Fort Kent, Aroostook County, M. L. Fernald 2289, 15 June 1898"; holotype GH!; isotypes CAN!, US!, NY!, BRY!, BM!

Distribution: Newfoundland, New Brunswick, Nova Scotia, Quebec, Ontario, and Maine.

Plants of this variety from the Farm River, south of James Bay, Ontario, have fasciculate leaflets and short pods. In the latter feature they simulate var. *chartacea* (Fassett) Barneby, which might best be regarded as only a disjunct phase of this variety.

12d. *Oxytropis campestris* ξ *melanocephala* Hook., Fl. Bor.-Amer. 1: 147. 1831.

= *O. maydelliana* Trautv.

Synonym: *O. maydelliana* ssp. *melanocephala* (Hook.) Porsild

Type locality: "Bear Lake to the Arctic Shores and Islands, Dr. Richardson; Capt. Sir J. Franklin and Capt. Back, Capt. Sir E. Parry, &c." (Hooker l.c.).

Type: "24 July 2–Augt [?] 1826. O. camp. ξ. Dr. Richardson"; lectotype (here selected) BM!; isolectotypes GH!, K Hooker! ("ξ. Arctic Sea. Richardson. Oxytropis campestris,").

Paratypes: "Capt. Parry. 2nd Voy. [and] Parry's 2nd Voy.," both at K Hooker!; and "Oxytropis campestris. Duke of York's Bay. Arctic Regions. Parry's 2nd Voyage," BM 45449! Several additional specimens from Parry's second voyage are also present at BM.

The Richardson isolectotype at K consists of two specimens, both with stipules pale and merely mottled with purple instead of purplish overall as in most specimens of *O. maydelliana*. Because they are, however, somewhat unusual among specimens of the species, they are not chosen as lectotype. Specimens at BM more closely represent the concept of the taxon. The isolectotype at K is mounted on a sheet with two collections by Capt. Parry from the second voyage, and a third collection by Simpson from the "Polar Sea." The Parry collections are apparent paratypes of ξ *melanocephala* Hook. An extraneous stem of *O. borealis* var. *hudsonica*, mounted on the same sheet, appears to belong to one of the Parry collections. On the lectotype specimen at BM the name "Dr. Richardson" was obviously added later as it is on most specimens attributed to him, and the date 1826 is correct for the second Franklin expedition. There is a second sheet at BM!, "1/147. Oxytropis campestris DC. River Rae," with the name Dr. Richardson written below the label, and bearing the notation, "Oxytropis campestris. DC. β sordida Lin." Possibly it is a paratype of var. *melanocephala.* Many of the specimens from Parry's second voyage designated as *O. campestris* are *O. maydelliana,* but some are *O. borealis* var. *hudsonica.*

12e. *Oxytropis campestris* **var. *minor* (Hook.) Welsh, comb. nov.,** based on "*Oxytropis uralensis* γ *minor* Hook., Fl. Bor.-Amer. 1: 146. 1831.

Synonym: *O. terrae-novae* Fernald; *O. campestris* var. *terrae-novae* (Fernald) Barneby (see *O. uralensis* for discussion of the reasons for this combination)

12f. *Oxytropis campestris* var. *speciosa* Torr. & A. Gray, Fl. N. Amer. 1: 341. 1838.

Based on: *O. campestris* γ *sulphurea* sensu Hook., Fl. Bor. Amer. 1: 147. 1831 (see below).

= *O. sericea* Nutt. var. *speciosa* (Torr. & A. Gray) Welsh

Type locality: "British America, west to the Pacific" (Torrey and Gray l.c.).

Type: "Dr. Hooker"; lectotype (here selected) NY!

Paratypes: "Ox. campestris γ sulphurea. Dr. Hooker's Fl. B. Am. Rocky Mountains. Drummond," at K Hooker! and "Oxytropis campestris γ. Frankl. Exp. Dr. Richardson," at BM!

The sheet at NY, communicated by Dr. Hooker, bears the notation, "Carlton House on the Saskatchewan to the Rocky Mountains, Drummond," and the initials E. P. S[heldon?]. The quote is identical to that for varieties α and δ in the *Flora,* but since Hooker did not cite a locality for γ *sulphurea,* the material sent to Gray by Hooker could have been taken by either Douglas or Richardson and not necessarily by Drummond. There are authentic specimens bearing the name "*sulphurea*" at BM, one by Douglas and the other by Richardson, and possibly a third by Richardson with the simple designation, "Oxytropis campestris γ." Probably the lectotype at NY was taken by one or the other of the two collectors, and not by Drummond. However, the specimen at K cited as paratype was collected by Drummond.

Hooker's brief description of γ *sulphurea,* "foliolis latioribus, spicis capitatis, floribus majoribus speciosis," characterizes this common plant of the western plains and foothills of the Rockies from far north in Canada south to Montana, Wyoming, and Idaho.

12g. *Oxytropis campestris* δ *spicata* Hook., Fl. Bor.-Amer. 1: 147. 1831.

= *O. campestris* (L.) DC. var. *spicata* Hook.

Type locality: "Between Carlton House on the Saskatchewan to the Rocky Mountains [Alberta], T. Drummond" (Hooker l.c.).

Type: "Oxytr. campestris δ. Carlton House. Fl. Bor. Am."; lectotype (here selected) K Hooker!

Hooker (1831) characterized δ *spicata* as "spicis elongatis, floribus remotioribus." That description, although short, matches the lectotype. There is only one sheet of *Oxytropis* at Hooker's herbarium at K that bears the designation δ and the locality information "Carlton House." The fact that Drummond is not indicated as collector on the sheet is apparently of little consequence as Hooker frequently failed to record collectors on his small herbarium labels or in his annotation of the specimens. The plants on that sheet clearly belong to what has passed in recent times under the name of *O. campestris* var. *gracilis* (A. Nelson) Barneby. That some plants sent by Hooker to Gray represented taxa other than var. *spicata* is unfortunate. It appears that Hooker clearly had two entities in mind when he described var. *spicata* and discussed var. *sulphurea.* Indeed, Barneby (1952: 279) masterfully summarized the problems of identification of specimens of var. *spicata* (as *O. campestris* var. *gracilis*) and var. *speciosa* (as *O. sericea* var. *spicata*). Much of the material exchanged by Hooker is, indeed, the larger-flowered phase (here termed var. *speciosa*) with fewer leaflets. Whether Hooker was responsible for sending wrongly labeled material that was segregated prior to its distribution is not known. If Drummond mixed his collection so as to include both varieties, he was not alone in mixing the two pale-flowered species of the plains of western Canada. The var. *spicata,* with its numerous leaflets and small flowers, grows in the general area occupied by the larger-flowered phase with fewer leaflets. Many botanists have made similar misinterpretations. The need to replace var. *spicata* with var. *speciosa* is an unfortunate but necessary change mandated as the result of study of the types.

12h. *Oxytropis campestris* var. *sulphurea* sensu Hook., Fl. Bor. Amer. 1: 147. 1831. non DC.

= *O. sericea* var. *speciosa* (Torr. & A. Gray) Welsh

Authentic specimens of *O. campestris* β *speciosa* Torr. & A. Gray: "2. O. *campestris.* β *sulphurea* on the red deer and eagle hills of the [illegible]. 1827," North America. D. Douglas, and "Oxytropis campestris γ, Frankl. Exp. Dr. Richardson" (both at BM!); and "Ox. campestris γ sulphurea. Dr. Hooker's Fl. B. Am. Rocky Mountains. Drummond" (at K Hooker!).

13. *Oxytropis deflexa* **var. *pulcherrima* Welsh & A. Huber, var. nov.** *O. deflexae* var. *foliolosae* (Hook.) Barneby aspectu similis sed in floribus majoribus, racemis latioribus et dense pilosis, et a var. *sericeae* Torr. & A. Gray in racemis compactis et floribus majoribus et purpureis differt.

Type: USA, **Utah**, Duchesne County: "T2N, R7W, S31 NW/NW, UB&M, head of Log Hollow, 1.8 mi due SW of Upper Stillwater Reservoir, Uinta Mts., gravelly subalpine meadow, common, limestone substrate, at ca 3294 m, 12 July 1994, A. Huber 1673"; holotype BRY!, duplicates to be distributed. Additional materials (paratypes): Utah, Duchesne County: Uinta Mountains, T2N, R7W, S31, 11 mi N of Tabiona, 12 July 1972; do, T2N, R6W, S18, divide between Rock Creek and Brown Duck Basin, at 3447 m, 28 August 1981, S. Goodrich & D. Atwood 16163; do, T2N, R7W, S30, 3 July 1978, S. Goodrich & L. Hart 11705; do, T1N, R8W, S1, head of Wedge Hollow, 6 July 1990, D. Atwood 13934. Utah, Summit County: Lost Creek Park, road from Hoop Lake to Spirit Lake, at 3050 m, 23 August 1977, K. Ostler 932. Utah, Daggett County: T2N, R17E, S11, 22.2 km SW of Manila, at 2815 m, 11 August 1983, S. Goodrich 19661. **Colorado**, Chaffee County: 0.7 mi NE of Cumberland Pass, T12 N, R4E, S12, at 3730 m, 17 August 1982, J. Peterson et al. 82-58. Colorado, Gunnison County: Virgina Basin, at 3691 m, 8 July 1946, C. L. Hayward 148; do, Cumberland Pass, at 3874 m, 23 July 1970, L. C. Higgins 3755; do, 9 July 1969, L. C. Higgins 2103; do, North ridge of Mount Belview, at 3750 m, 5 July 1988, L. C. Marvin 3105. All specimens at BRY!

Plants of var. *pulcherrima* may be distinguished from all other North American materials of the *deflexa* complex by their compact racemes (remaining so in fruit), larger flowers (hence broader racemes), and short, plump pods that tend to have an abrupt shoulder beyond the stipe. Their bipartite distribution from alpine sites in the Uinta Mountains and similar, but higher, areas in the southwestern Colorado Rockies is unique among *Oxytropis* species. This is material that has been regarded in contemporary treatments of the genus in North America as var. *deflexa*. Specimens of var. *deflexa* from Siberia, at least those examined by me, have elongate racemes, smaller flowers, and more slender pods.

14. *Oxytropis foliolosa* Hook., Fl. Bor.-Amer. 1: 146. 1831.

= *O. deflexa* var. *foliolosa* (Hook.) Barneby

Type locality: "From Carlton-House to the Rocky Mountains, in lat. 54°" (Hooker l.c.).

Type: "Ox. foliolosa Hook. Fl. Bor. Am. Rocky Mountains, Drummond" Alberta, Canada; holotype K Hooker!; isotype NY!

The holotype consists of two flowering specimens representing the common acaulescent or subcaulescent phase of var. *foliolosa*. The upper specimen displays immature fruit.

There are collections of *O. deflexa* var. *sericea* Torr. & A. Gray at K by Nuttall ("Oxytropis deflexa. R. Mts.") and by Drummond ("Saskatchewan. Drummond. Ox. deflexa. DC.").

15. *Oxytropis hookeriana* Nutt. in Torr. & A. Gray, Fl. N. Amer. 1: 340. 1838.

= *O. lambertii* Pursh var. *lambertii*

Type: "Oxytropis * Hookeri. O. Lamberti β Hook. 147. Platte plains," Nuttall s.n. 1834; holotype BM Nuttall!

The specimen at BM has "Platte plains" written on the back of the sheet. It seems apparent that Nuttall hoped to honor Hooker by providing a name for what he took to be the concept of *O. lambertii* β, a plant that is a phase of *O. campestris* scarcely related to *O. lambertii*.

16. *Oxytropis ixodes* Butters & Abbe, Rhodora 45: 2, tab. 745, fig. 1–6. 1943.

= *O. borealis* DC. var. *viscida* (Nutt.) Welsh

Type: Minnesota, "slate cliffs on north side of a high hill 1/2 mi. west of the outlet of South Fowl Lake, Cook County, F. K. Butters, E. C. Abbe, & G. W. Burns 611, 27 June 1940"; holotype MIN; isotype GH!, NY!, PH!, US!, UC!, DAO!, BRY!, BM!

17. *Oxytropis lagopus* Nutt., J. Acad. Nat. Sci. Philadelphia 7: 17. 1834.

Type: Sources of the Missouri, N. B. Wyeth s.n. 1833; holotype BM Nuttall!; isotypes NY!, PH!, K!

The specimen at BM has a label of a typical Nuttall collection, "Oxytropis * lagopus—Sources of the Missouri." It is mounted on a sheet with a collection from "Rocky Mts, near the Platte," by Dr. Parry. The Royal Botanic Garden material consists of a single caudex branch and two inflorescences.

18. *Oxytropis lambertii* Pursh, Fl. Amer. Sept., 740. 1813.

Type: "On the Missouri, on the bluffs from the Maha village to the Poncars, Louisiana [NE Nebraska or adjacent South Dakota or Iowa], Bradbury s.n. 1811"; lectotype PH! (Barneby, Proc. Calif. Acad. Sci. IV. 27: 285. 1952, as type); isotype BM!

The sheet at BM is labeled "Louisiana. J. Bradbury 1811–12."

18a. *Oxytropis lambertii* β. Hook., Fl. Bor.-Amer. 1: 147. 1831.

= *O. campestris* (L.) DC. var. *davisii* Welsh

Type locality: "Dry banks on Red River and Saskatchawan, (Douglas,) to the Prairies in the vallies of the Rocky Mountains. Drummond" (Hooker l.c.).

Type: "Oxytropis lambertii β. Dr. Hooker"; holotype K! (see discussion below); isotype NY!

Authentic specimen: "Oxytropis Lambertii β. Frankl. Exp. Dr. Richardson" (BM!).

Neither Douglas's nor Drummond's materials with the unequivocal designation *O. lambertii* β have been seen at either K or BM. There is at K Hooker, however, a collection by Drummond (cited below as a possible paratype of *O. uralensis* γ *minor* Hooker, q.v.) that bears the penciled notation "Ox. Lamberti??" It appears to be *O. campestris* var. *davisii* Welsh. The Richardson collection at BM (authentic specimen cited above) almost certainly is that taxon also. A second sheet at K Hooker bears three collections, two small plants by Drummond, two taller plants presumed to be by Douglas, and a third extraneous collection by Percival. The first and second are var. *davisii*, and there is a penciled notation, "Ox. Lambertii Pursh." That Hooker misunderstood that at least some part of his var. *minor* and his var. β were conspecific indicates the problem he had in dealing with plants from such diverse areas as those found in North America, plants he had not seen in the field. Designation of a lectotype for the material is probably moot, since the material was not given more than alphabetical designation. Perhaps these sheets, as interpreted herein, will lay to rest the name *O. lambertii* β. Had there been an epithet applied, it would have precluded the use of the name *davisii*.

18b. *Oxytropis lambertii* β *leucophylla* Nutt. in Torr. & A. Gray, Fl. N. Amer. 1: 339. 1838, pro syn.

= *O. lambertii* ε. (see below)

18c. *Oxytropis lambertii* ε. Torr. & A. Gray, Fl. N. Amer. 1: 339. 1838.

= *O. lagopus* var. *atropurpurea* (Rydb.) Barneby pro parte et *O. nana* Nutt. pro parte

Synonym: *O. lambertii* β *leucophylla* Nutt.

Authentic specimen: "Oxytropis * *leucophylla*. R. Mts.," Nuttall s.n. 1834, BM Nuttall!

The authentic specimen has the information "Rocky Mts. Nuttall's Herb." written on the reverse side, and the following notation on the front: "Oxytropis leucophylla Nuttall! [Oxytropis] Lamberti Pursh var. glabrata Torr. & Gr. Fl. N. America 1: p. 339." The name was published as a synonym by Torrey & A. Gray (l.c.), based on a manuscript provided by Nuttall. They characterize the plant by the following description, but evidently did not see the material: "ε. very dwarf, canescently woolly; the leaflets shorter and about 5 pairs; scape scarcely longer than the leaves; flowers capitate or nearly so; calyx densely woolly; bracts small and short; wings emarginate.—*O. Lamberti* β *leucophylla*, Nutt. mss," from "Plains of the Platte." Barneby (1952: 304) noted that there "seem to be no corresponding specimens either at Philadelphia or in the herbaria of Gray and Torrey." He therefore surmises that the plant in question belongs to *O. lagopus* var. *atropurpurea.* There is a sheet at BM bearing Nuttall's characteristic label with the name "Oxytropis * *leucophylla*" in Nuttall's handwriting. The two plants on the sheet apparently belong to two different taxa, the smaller one to *O. lagopus* var. *atropurpurea* as surmised by Barneby, and the second larger one to *O. nana* of Nuttall (or perhaps, but unlikely, a dwarf specimen of *O. sericea,* my first impression).

19. *Oxytropis mollis* Nutt. ex A. Gray, Proc. Amer. Acad. Arts 6: 235. 1864. pro syn.

=*O. borealis* var. *viscida* (Nutt.) Welsh

Authentic specimen: "Oxytropis mollis. O. Ochroleuca Led. Altai proxima . . . R. Mts. Oregon," Nuttall s.n. 1834 (BM Nuttall!).

20. *Oxytropis multiceps* Nutt. in Torr. & A. Gray, Fl. N. Amer. 1: 341. 1838.

Type locality: "Summit of lofty hills in the Rocky Mountain range, towards Lewis's River [S. Wyoming], Rocky Mts. Nuttall" (Torrey and Gray l.c.).

Type: "Oxytropis (Physocalyx) *multiceps.* R. Mts." T. Nuttall s.n. 1834; holotype BM Nuttall!; isotypes NY!, GH!, K Hooker!

The two specimens at BM are mounted on a sheet with collections by J. M. Coulter and M. E. Jones. The Nuttall material bears three labels: "***Physocalyx** * *multiceps* R. Mts." and two others. The second label makes comparisons with Old World species that the proposed new genus and species could not be, and the third label contains a brief description, "Cal. inflatus, apice 5-fidus, legumine includens." Nuttall was at least entertaining the idea that the plant represented a new genus.

Distribution: Colorado, NE Utah, SW Wyoming, and W Nebraska.

The accrescent calyces, broad bracts, and few flowers are characteristic for the species, which stands alone in the genus in North America in its morphology.

20a. *Oxytropis multiceps* var. *minor* A. Gray, Proc. Amer. Acad. Arts 20: 2. 1884.

= *O. multiceps* Torr. & A. Gray

Type: Clear Creek County, Colorado, C. C. Parry 991, 1861; lectotype GH! (designated by Barneby, Proc. Calif. Acad. Sci. IV. 27: 220. 1952); isolectotype NY!

Paratype: "Rocky Mountain Alpine Flora, Lat. 39°–41°. No. 144. E. Hall & J. P. Harbour, Colls. 1862"; BM!

21. *Oxytropis nana* Nutt. in Torr. & A. Gray, Fl. N. Amer. 1: 340. 1838.

Type: Plains of the Platte in the Rocky Mountain Range [Wyoming], T. Nuttall s.n. 1834; holotype BM Nuttall!; isotypes NY!, PH!

Distribution: Drainage of the North Platte and Cheyenne rivers, westward to the Wind River Mountains, Albany, Carbon, Converse, Fremont, Natrona, Platte, and Sweetwater counties, Wyoming; endemic.

This is a beautiful species of clays, shales, and gravelly bluffs and ridge tops endemic to Wyoming. Barneby (1952) postulated that it might have arisen through hybridization of *Oxytropis sericea* and *O. multiceps,* a likely supposition. Flower colors are variable in a given population from pale pinks through lavender and purple, and white-flowered populations are known. A contribution from *O. lambertii* is also suggested by the presence of incipiently malpighian hairs in some specimens. The relationship to segregates of *O. besseyi* postulated by Isely (1983) seems tenuous at best. The relegation of *O. nana* to that species might require a realignment of other taxa as well, including combination of *lambertii, sericea, campestris,* and even *multiceps.* Such a proposal is, of course, absurd. Taxonomy must be both practical and reflect biological reality.

22. *Oxytropis plattensis* Nutt. in Torr. & A. Gray, Fl. N. Amer. 1: 340. 1838.

= *O. lambertii* var. *lambertii*

Type: "Oxytropis * Plattensis, R. Mts. Platte," Nuttall s.n. 1834; holotype BM Nuttall!; isotype NY!

The holotype at BM consists of a single plant cut from another sheet. It is typical of the Great Plains phase of *O. lambertii.*

23. *Oxytropis podocarpa* A. Gray, Proc. Amer. Acad. Arts 6: 234. 1864.

Type locality: "Labrador, Arctic regions, and Rocky Mountains, lat. 49°" (Gray l.c.).

Types: Labrador (Schweinitz), Arctic America (Richardson?), *O. arctica* δ *inflata* Hook. (Drummond), and Alberta (Bourgeau). The Schweinitz and Bourgeau specimens at GH! are cotypical, both having been used by Gray in characterization of the species. However, the species was lectotypified by Fernald (Rhodora 30: 154. 1928) on the Schweinitz collection from Laborador. The remaining specimens are considered to be paratypes.

Paratypes: "Highest summits of the Rocky Mts., Drummond" s.n, K!, type of *O. arctica* δ *inflata* Hook., q.v.; "Oxytropis arctica δ R. Br. Arctic America. Frankl. Exp.," K Hooker!

Distribution: Rocky alpine ridges and coastal shores in Colorado, Wyoming, Montana, Alberta, Northwest Territories, Ungava Peninsula, Labrador, and Baffin Island.

The bladdery-inflated stipitate pods of *Oxytropis podocarpa* are characteristic of this and few other oxytropes. The folded, falcate leaflets are useful in distinguishing this from other closely related mat- or mound-forming species, such as *O. nigrescens,* in vegetative condition.

24. *Oxytropis sericea* Nutt. in Torr. & A. Gray, Fl. N. Amer. 1: 339. 1838.

Type: Rocky Mountains toward the sources of the Oregon [S Wyoming], T. Nuttall s.n., 1834; lectotype NY! (Barneby, Proc. Calif. Acad. Sci. IV, 27: 272. 1952).

24a. *Oxytropis sericea* **var.** *speciosa* **(Torr. & A. Gray) Welsh, comb. nov.,** based on "*Oxytropis campestris* β *speciosa* Torr. & A. Gray, Fl. N. Amer. 1: 341. 1838, this in turn based on *O. campestris* γ *sulphurea* sensu Hook., Fl. Bor. Amer. 1: 147. 1831.

Missapplied name: *O. sericea* var. *spicata* sensu Barneby, Leafl. W. Bot. 5: 111. 1951.

Distribution: Yukon, British Columbia, Alberta, Saskatchewan, Manitoba, Montana, Idaho, and Wyoming.

Members of this variety are characterized by ochroleucous flowers with immaculate keel. In general aspect they simulate the partially sympatric *Oxytropis campestris* var. *spicata,* from which they may be distinguished by fewer leaflets and generally larger flowers. Alpine phases of *O. campestris* var. *cusickii* approach var.

speciosa both in flower size and color. Mainly var. *speciosa* does not occur in highlands inhabited by var. *cusickii*, but the similarities of the two varieties should not be discounted. Apparent hybrids are known between this and *O. campestris* var. *davisii* in northeastern British Columbia.

25. *Oxytropis splendens* Douglas ex Hook., Fl. Bor.-Amer. 1: 147. 1831.

Type locality: "On limestone rocks of the Red River, and south toward Pembina [S Manitoba]. Douglas" (l.c.).

Type: "On Limestone rocks of the Red River and on the south towards Pembina, 1827, α Ox. splendens. Douglas"; lectotype (here selected) K Hooker!; isolectotypes OXF! (photo BRY!), BM! ("O. splendens. Dry soils on the plains of Red River. 1827. Douglas s.n."; 2 sheets). The two sheets at BM are both by Douglas and represent α *vestita*, the typical phase of the species.

The lectotype at K bears a label with almost the exact information as the published type locality. It is mounted on a sheet with a specimen designated "β," and with the label information "Rocky Mts. Richardson." A better choice for lectotype of var. β is on a second sheet (see below).

25a. *Oxytropis splendens* α *vestita* Hook., Fl. Bor.-Amer. 1: 148. 1831

= *O. splendens* Douglas

Type locality and type: As for the species.

25b. *Oxytropis splendens* β *richardsonii* Hook., Fl. Bor.-Amer. 1: 148. 1831.

= *O. splendens* Douglas

Type locality: "From Cumberland-House on the Saskatchewan, north to Fort Franklin and the Bear Lake, and West to the dry prairies of the Rocky Mountains. Dr. Richardson; Drummond" (Hooker l.c.).

Type: "278. Oxytropis oxyphylla. Dr. Richardson" s.n. in 1821; lectotype (here designated) K Hooker!; isolectotypes NY!, *O. oxyphylla* of Richardson, GH!

Paratype: "Fort Franklin to the Rocky Mts. Drummond. β. Ox. Splendens. Dougl. Hook. Fl. B. Am.," K Hooker!

The lectotype has three specimens, each designated "β." The label "278. Oxytropis oxyphylla" is affixed across the base of the middle specimen; adjacent to the left one is "Bear Lake," and below the specimen at the right is the collector's name, "Dr. Richardson." The name "O. oxyphylla," in the sense utilized by Richardson in the botanical appendix to Franklin's first journey (1823), is clearly the basis for Hooker's β. *richardsonii*.

The Drummond syntype consists of a beautiful plant with several flowering stems and numerous leaves, and a fruiting raceme and peduncle.

Barneby (1952) notes:

> Hooker recognized from the first a typical α *vestita*, "valde hirsuto-sericea, bracteis hirsutissimis calyce multo longioribus," described from Douglas's Red River plants, and a β *richardsonii*, "minus hirsuta, bracteis vix longitudine calycis," collected between the Saskatchewan River and the Rocky Mountains.

Plants of the two types pass into each other by degree and have not been recognized at taxonomic rank in recent times.

26. *Oxytropis uralensis* sensu American authors, non (L.) DC.

North American specimens at BM and K bearing this name are a mixture of (a) *O. arctica* R. Brown var. *arctica* (eglandular, with large, pink-purple flowers); (b) *O. borealis* var. *hudsonica* (Greene) Welsh (glandular, the calyx teeth short and purplish flowers (see "7/1834.7 Oxytropis Uralensis. British North America. Dr. Richardson 1819–22, BM!," and "Repulse Bay. Parry's 2nd Voyage, BM!"); (c) "Arctic Regions. Oxytropis Uralensis. Repulse Bay. Parry's 2nd Voyage"); (d) *O. maydelliana* Trautv. (ochroleucous flowers, with stipules castaneous); and (e) *O. campestris* var. *minor* (Hook.) Welsh (including var. *terrae-novae*, flowers pink purple, eglandular).

26a. *Oxytropis uralensis* α in Hook., Fl. Bor.-Amer. 1: 146. 1831.

= *O. arctica* R. Brown var. *arctica*

Locality: "Arctic regions and islands. Dr. Richardson; Capt. Parry &c." (Hooker l.c.).

Authentic specimen: "O. uralensis α Frankl. Exp. Dr. Richardson," BM!

Hooker's (1831) use of *Oxytropis uralensis* α in his discussion of habitat merely indicated acknowledgment of the taxon in the sense of Old World materials. However, an authentic specimen at BM with that label information is *O. arctica* sens. str. (see above).

26b. *Oxytropis uralensis* var. *subsucculenta* Hook., Fl. Bor.-Amer. 1: 146. 1831.

= *O. borealis* DC. var. *borealis*

Type locality: "Arctic seashore, to the east of the Mackenzie River" (Hooker l.c.).

Type: "O. uralensis β. 126. H. Sea Coast. Dr. Richardson"; lectotype (here designated) BM!

The lectotype at BM is mounted with *O. uralensis* α, i.e., *O. arctica* R. Br. var. *arctica*. A possible syntype of β *subsucculenta* Hook. is also present at BM, with the label "British North America. Dr. Richardson 1819–22." Above the label is a pencil notation, "cut from sheet of *Oxytropis campestris*."

26c. *Oxytropis uralensis* var. *arctica* (R. Br.) Ledebour, Fl. Ross. 1: 594. 1842.

Basionym: *Oxytropis arctica* R. Br.

= *O. arctica* R. Br. var. *arctica*

26d. *Oxytropis uralensis* γ *minor* Hook., Fl. Bor.-Amer. 1: 146. 1831.

= *O. campestris* var. *minor* (Hook.) Welsh (see 12e above)

Type locality: "Dry hills and prairies of the Rocky Mountains. Mr. Drummond. Labrador. Mr. Morrison" (Hooker l.c.).

Type: "Labrador. O. uralensis γ. Morrison"; lectotype (here designated) K Hooker!

The International Code of Botanical Nomenclature allows recognition of a taxon based on discordant material where the name can be applied to at least one of its parts. Hence, var. *minor* is not to be rejected simply because the specimens on which it was based represent more than one taxon. Evidence to support the assignment of the name to the Labrador material is unequivocal, while its application to materials from western Canada is problematical.

The lectotype at K consists of two specimens, one flowering and the other in fruit. They were mounted previously with plants of another species, which have been removed by cutting the sheet. The specimens both bear the notation "γ," and the sheet contains the annotation "O. uralensis γ Fl. Bor. Am. sed certi fructu ab Uralensi diversum," the author unknown. Barneby (1952) was unable to resolve the application of the name but noted: "The problem is nomenclaturally important in that var. *minor* could prove to be the earliest name in its category for either *O. viscida* var. *hudsonica* or *O. campestris* var. *terrae-novae.*" The Labrador specimens cited with the original description are *O. campestris* var. *terrae-novae* in a modern sense and are here selected as the lectotype for the taxon.

Two small specimens at K Hooker! bearing the label "Saskatchewan. Drummond" appear to be var. *davisii*, but one cannot be certain of their provenance or that they represent the material designated by Hooker as var. *minor.* They are mounted on a sheet with two additional specimens, apparently var. *davisii* also, but probably collected by Douglas. Possibly all four specimens formed the basis for still another of Hooker's plants, *O. lambertii* β (q.v.). A more convincing collection possibly included by Hooker within var. *minor*, at K, is labeled "Astragalus uralensis. Dry mountain prairies & low hills. Drummond." It is a possible syntype of var. *minor* and appears to be var. *davisii* Welsh. There is no certainty, however, that the specimen is part of what Hooker indicated as var. *minor.*

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SALTATION IN SNAKES WITH A NOTE ON ESCAPE SALTATION IN A *CROTALUS SCUTULATUS*

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Key words: Crotalus scutulatus, *escape saltation, behavior.*

Escape saltation and aggressive saltation have been reported in relatively few snakes (Gans and Mendelssohn 1971, Klauber 1972, Gans 1974, Armstrong and Murphy 1979, Gasc 1994). These reports range from the incredulous to the well documented. Gasc (1994) relates an unbelievable case of jumping in *Atropoides* (=*Porthidium*) *nummifer* in which individuals "tend to jump, either when they hit a prey or *to clear a height of up to 3 ft (1 m)*, starting from a low point [emphasis added]." Certainly *A. nummifer* may jump; however, in their decades of experience with hundreds of these snakes in both the wild and captivity, W. Lamar, L. Porras, and A. Solorzano have never seen nor heard of this behavior (personal communication). It is possible that *A. nummifer* may appear to jump as they strike from an arboreal perch (i.e., a log) and fall to the ground (L. Porras personal communication).

The best reports of ophidian saltation are those of Gans and Mendelssohn (1971) and Gans (1974). These authors analyzed *Bitis caudalis* jumping behavior in terms of stimulus and biomechanics. They determined that *B. caudalis* weighing less than 23.5 g, with a body temperature between 31°C and 37°C, were able to jump using sidewinding locomotion. This type of saltation is energetically expensive, and jumping snakes tire quickly.

Believable reports of rattlesnake saltation are relatively few. Klauber's (1972) reports consist primarily of exaggerated accounts of rattlesnakes jumping while striking at either prey or man. However, one of his reports cannot be ignored:

> Dr. R. B. Cowles told me that he was always skeptical of stories of rattlesnakes leaving the ground in the course of a strike, until he saw this done two or three times by an angry southwestern speckled rattler (*Crotalus mitchellii pyrrhus*). The snake was on pavement and struck for more than its full length.

The only other report of rattlesnakes jumping is of *C. scutulatus salvini* which "struck so violently that their entire body appeared to be momentarily air borne" (Armstrong and Murphy 1979). Neither of these reports discusses the biomechanics of how these snakes jumped. Since both accounts are of aggressive saltation, and neither of the species typically utilizes sidewinding locomotion (Cowles 1956, Klauber 1972), the biomechanics involved in rattlesnake saltation is likely different from that in *B. caudalis.* Here we report an instance of escape saltation in a wild *C. s. scutulatus.* Although our observations are anecdotal, we believe they offer important insight into the biomechanics of rattlesnake jumping.

On 4 September 1993 we observed an unusual flight behavior by a wild *C. s. scutulatus* in the Hualapai Mountains, Mojave County, AZ. When approached, the snake lunged forward using its tail as the origin of force. This lunge was powerful enough to cause the snake's entire body to lift off the ground (Fig. 1). Actual forward movement from this "jump" was minimal, and the snake recoiled into a series of tight S-curves and jumped again. This type of saltation was observed a total of four times. None of the four jumps were directed toward a person, and the snake's mouth appeared to remain closed.

Of the four types of snake locomotion, this jumping behavior could only be accomplished using concertina, in which the tail is the main point of force during foward movement. Klauber (1972) noted that rattlesnakes use concertina movement for slow progression in open areas and where restraints are involved (i.e., smooth

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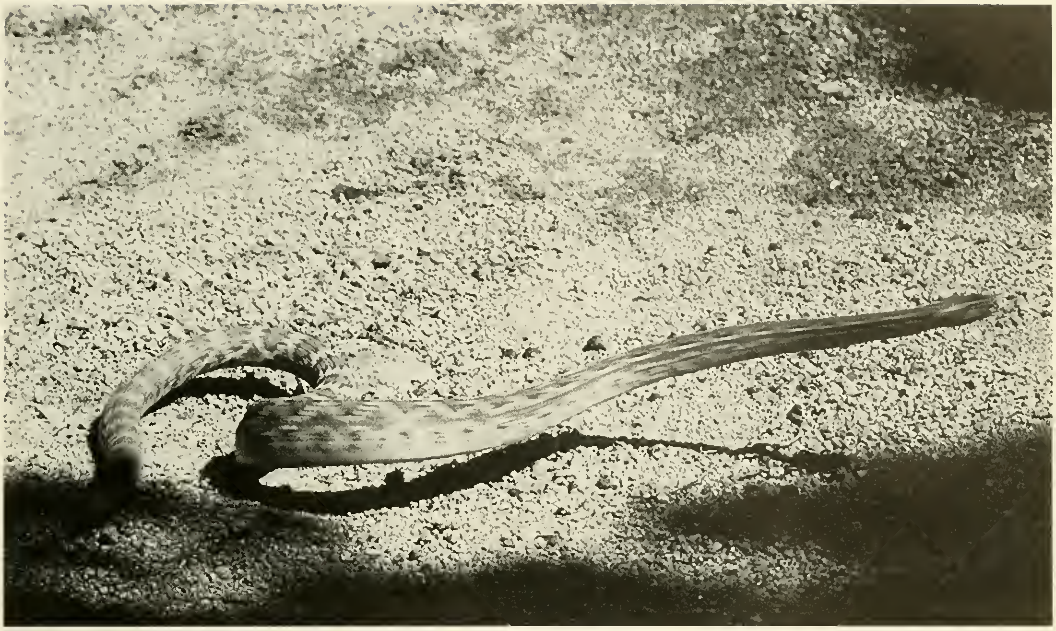

Fig. 1. *Crotalus s. scutulatus* exhibiting escape saltation. Photograph taken just before the tail left the ground.

surface or narrow channel). Neither of these circumstances was applicable to this particular situation. The use of concertina locomotion rather than sidewinding as a basis for jumping in this snake is understandable as an antipredator response. *Crotalus s. scutulatus* typically utilize quick serpentine locomotion during flight; Klauber (1972) noted they are rather clumsy sidewinders. By reducing the number of pressure points to one (e.g., the tail), the snake changed from serpentine to concertina locomotion. Whether this change is an effective use of energy remains to be tested. However, given the short distance the snake traveled, it would appear the relative energy cost would be high.

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A TRAP FOR BLUE GROUSE

Eric C. Pelren[1] and John A. Crawford[1]

Key words: Blue Grouse, Dendragapus obscurus, *interception trap, Oregon, trapping success, walk-in trap.*

Numerous techniques have been developed to capture Blue Grouse (*Dendragapus obscurus*) for scientific purposes, but efficacy differs among methods and is influenced by terrain, habitat conditions, and wariness of birds. Zwickel and Bendell (1967) captured over 1200 Blue Grouse in British Columbia between 1950 and 1967 with a "noosing pole." Zwickel estimates that 10,000–15,000 Blue Grouse have been captured with nooses in parts of their range from Alaska to California and from Alberta to Colorado (personal communication). However, noosing poles and other approach-based techniques may not be effective for capturing Blue Grouse in areas where birds do not permit close approach by humans, where baiting is ineffective, or where topographic or habitat conditions preclude use of drive traps. Consequently, additional methods are needed to supplement existing techniques.

Henderson (1960), Standing (1960), and Bauer (1962) used walk-in traps to capture over 520 Blue Grouse in north central Washington from 1956 to 1961. We developed a similar trap for spring and summer capture of adult and juvenile Blue Grouse in northeastern Oregon where the wary nature of the birds made noosing poles and other approach-based capture techniques ineffective. Our objective is to describe the design and success rate of a walk-in trap for Blue Grouse and to present this trap as a viable alternative when approach-based capture methods are ineffective.

We used a walk-in style trapset designed to intercept the movement of birds through the trapping area and guide these individuals along wire fences into funnels connected to trap boxes (Gullion 1966). Our trapsets usually consisted of three open-bottomed boxes (range 1–7) connected by fences (Fig. 1) and required 1–3 h for placement. Trap boxes were constructed in approximately 45 min from plastic or metal wire or netting. A primary concern in choosing trap material is that birds may injure themselves on the traps. Fish netting and/or vegetation on top of the box reduces the possibility of injury (Henderson 1960, Standing 1960, Bauer 1962). Size and placement of entrance funnels is critical. We fitted 5-cm hexagonal-weave chicken wire funnels to the entrance holes; funnels had inner-opening dimensions of 6 cm width × 10 cm height if the trap was intended primarily for immatures and 8 cm width × 12 cm height if the trap was intended primarily for adult birds.

Successful traps were constructed where birds had been located repeatedly within a 5- to 10-m^2 area. Fences between boxes were shorter where grouse were more highly localized to increase the concentration of trap boxes in those areas.

We captured 140 grouse in 2327 trap(set)-days during summers 1991, 1992, and 1993 at rates of 23, 19, and 12 trap-days/capture, respectively (Table 1). Increased trapping efficiency in 1992 and 1993 was likely a product of refined trapping techniques, experience of trappers, and knowledge of bird movements. Henderson (1960) achieved capture rates of 7 and 8 trap-days/capture in 1958 and 1959, respectively. Variations in capture success rates may be influenced by grouse population density and distribution. Habitats in which grouse are evenly distributed are more difficult to trap than areas in which grouse congregate in dense clumps.

Many variations in design, material, construction, and placement of walk-in traps exist. Flexibility, creativity, and an understanding of the system in which trapping efforts take place are critical for successful application of this trap to specific conditions.

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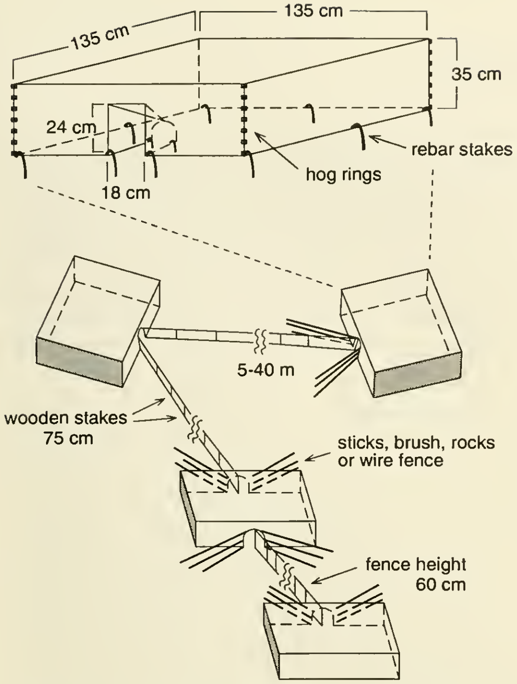

Fig. 1. Interception trap design incorporating V-shaped and linear arrangement for capturing Blue Grouse.

The noosing pole is an effective method for capturing Blue Grouse in much of its range. This technique requires significantly less time, manpower, and money than traps; however, in areas where birds are too wary to be approached and captured by noosing pole, interception traps may provide a viable alternative capture technique for Blue Grouse.

ACKNOWLEDGMENTS

TABLE 1. Blue Grouse interception trap capture statistics, June through August 1991, 1992, and 1993, in Wallowa County, OR.

	Year			
	1991	1992	1993	Total
Number of birds captured	27	50	63	140
Trap-days	618	941	768	2327
Trap-days/capture	23	19	12	17

This study was funded by the U.S. Forest Service and Oregon Department of Fish and Wildlife (ODFW). Special thanks go to ODFW Wallowa District Biologist Vic Coggins and his assistant Pat Matthews for technical support and suggestions during the trapping process. Trapping assistants Mark Porter and Jim Wach helped to refine our technique, and Fred Zwickel provided valuable input during the editing process. This is Oregon Agricultural Experiment Station Publication No. 10,355.

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BOOK REVIEW

Mountains and plains: the ecology of Wyoming landscapes. Dennis H. Knight. Yale University Press, New Haven and London. 1994. xi, 338 pp., illus. $40 hardback.

Many books describe the landscapes and ecology of subregions of the United States. This book provides a detailed description and ecological interpretation of Wyoming and adjacent areas. Although this region has long been a magnet, drawing national and international visitors to Yellowstone National Park, Teton National Park, the Black Hills, Devil's Tower National Monument, and to the expansive, sparsely populated plains and mountains that lie between those public attractions, this book provides more detail and a more holistic overview of the region than any existing reference designed for public consumption. Unusually well illustrated and handsomely designed, *Mountains and Plains* will appeal to and enrich the understanding of any thoughtful visitor to this land of natural wonders.

The author, Dennis H. Knight, has distilled for the reader a delightful mixture of landscape images and informative facts from his teaching and research experiences of over 30 years in the natural landscapes of Wyoming. Knight has written the book with interested laymen in mind. Roughly 120 carefully selected, well-reproduced photographs enrich the text. Many of the photos are masterfully selected to illustrate a puzzling or unexpected relationship. The photographs made my first "glance" at the book a rewarding four-hour experience! Numerous photos and their brief captions so inflamed my curiosity that I had to search the text for the author's well-researched comments before I could continue on. In keeping with his objective of writing for laymen, Knight uses only common names for animals and plants in the text, but well-organized appendices permit interested professionals to quickly link an unambiguous Latin binomial to any given common name. In the same vein, the author cites supporting references in such a way that the flow of the narrative is not broken, but interested scholars can readily determine where detailed studies of particular problems are published. The brief but clear explanations in the text are startlingly well supported by a massive body of references (over 1150 original sources cited).

Knight, a past president of the Ecological Society of America and a science advisor to numerous management agencies in the nation, has obviously poured many months of intense effort into *Mountains and Plains*. The entire book is carefully integrated and clearly written. His manuscript has been artfully and professionally assembled into a handsome, durable hardback volume by Yale University Press. Photographs are clearly reproduced and tastefully integrated into an essentially error-free text. The background sections of the book (Chapters 1 and 2) are supported by a variety of maps that permit the reader to quickly determine climatic, geologic, edaphic, and land ownership status at any geographic point in the area of concern.

Mountains and Plains is a book that anyone concerned with the natural history or management of Wyoming (or nearby) landscapes should own. Interested laymen will find the book to be informative and reliable. Managers of natural resources in the area will find the volume to be an essential companion in the field or at the desk. The price is modest for a hardback book of such sturdiness. Both Knight and Yale University Press are to be commended for a valuable contribution to our understanding of the natural environments in that area where the High Plains encounter the Rocky Mountains.

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INFORMATION FOR AUTHORS

The *Great Basin Naturalist* welcomes previously unpublished manuscripts pertaining to the biological natural history of western North America. Preference will be given to concise manuscripts of up to 12,000 words. Simple species lists are discouraged.

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Vol. 55, No. 3, July 1995

CONTENTS

Articles

Benthic community structure in two adjacent streams in Yellowstone National Park five years after the 1988 wildfires . . . . G. Wayne Minshall, Christopher T. Robinson, Todd V. Royer, and Samuel R. Rushforth **193**

Effects of browsing by native ungulates on the shrubs in big sagebrush communities in Yellowstone National Park . . . . Francis J. Singer and Roy A. Renkin **201**

Soft sediment benthic macroinvertebrate communities of the Green River at the Ouray National Wildlife Refuge, Uintah County, Utah . . . . Eric R. Wolz and Dennis K. Shiozawa **213**

Alpine vascular flora of the Tushar Mountains, Utah . . . . Alan C. Taye **225**

Ecology of *Celtis reticulata* in Idaho . . . . Ann Marie DeBolt and Bruce McCune **237**

Mimulus evanescens (Scrophulariaceae): a new annual species from the northern Great Basin . . . . Robert J. Meinke **249**

Morphological and host-symbiont studies of *Trichodina tenuiformis* and *Apiosoma campanulatum* infesting mottled sculpin (*Cottus bairdi*) from Provo River, Utah . . . . Ying Qi and Richard A. Heckmann **258**

Effects of horse grazing in spring on survival, recruitment, and winter injury damage of shrubs . . . . Dennis D. Austin and Philip J. Urness **267**

North American types of *Oxytropis* DC. (Leguminosae) at The Natural History Museum and Royal Botanic Garden, England, with nomenclatural comments and a new variety . . . . S. L. Welsh **271**

Notes

Saltation in snakes with a note on escape saltation in a *Crotalus scutulatus* . . . . Breck Bartholomew and Robert D. Nohavec **282**

A trap for Blue Grouse . . . . Eric C. Pelren and John A. Crawford **284**

Book Review

Mountains and plains: the ecology of Wyoming landscapes *Dennis H. Knight* . . . . Kimball T. Harper **286**

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CLASSIFICATION OF THE RIPARIAN VEGETATION ALONG A 6-KM REACH OF THE ANIMAS RIVER, SOUTHWESTERN COLORADO

Gillian M. Walford[1] and William L. Baker[2,3]

ABSTRACT.—Riparian ecosystems are important components of landscapes, particularly because of their role in biodiversity. A first step in using a "coarse-filter" approach to riparian biodiversity conservation is to determine the kinds of riparian ecosystems. These ecosystems vary substantially in plant species composition along a single river reach, as well as between rivers, and yet the river-reach scale has received little attention. We sampled the vascular plant composition of 67 contiguous patches of riparian vegetation along a reach of the Animas River, in southwestern Colorado's San Juan Mountains, that is relatively undisturbed by human land uses. Using cluster analysis and detrended correspondence analysis, we identified eight riparian community types along the reach. Using a new technique, we combined overstory size-class data and understory cover data to identify community types. The eight community types, which are in part the products of past floods, are spatially arranged along the reach in relation to variation in valley morphology, tributary location, and geomorphic landforms. These eight community types do not necessarily represent successional stages of a single potential vegetation type. This study at the river-reach scale suggests that sampling and analysis, as well as conservation, may need to be tuned to the scale of patchiness produced by flood disturbances in the riverine landscape, since vegetation varies significantly at this scale.

Key words: riparian vegetation, Rocky Mountains, Colorado, multivariate analysis.

Riparian vegetation provides several important functions in landscapes, and riparian communities have thus been a focus for conservation. Riparian vegetation contributes to water quality, stream bank stability, and healthy fish habitat (Johnson et al. 1985, Malanson 1993). Riparian vegetation also provides cover and forage for wildlife that is particularly important in the arid portions of North America (Knopf 1985). The idea of a "coarse-filter" approach to biodiversity conservation is that by preserving viable communities, associated species also will be preserved (Hunter 1991, O'Connell and Noss 1992).

Classification of vegetation communities is an essential first step in implementing this coarse-filter conservation approach, but classification of riparian vegetation in the Rocky Mountains is incomplete. The montane and subalpine riparian zones of Colorado's western slope have been classified (Baker 1989). Riparian community type classifications for U.S. Forest Service lands in Utah and parts of Idaho and Wyoming are available (Mutz and

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Graham 1982, Youngblood et al. 1985a, 1985b, Padgett et al. 1989). A riparian-wetland classification and key were produced for Montana (Hansen et al. 1991), and other classifications are available for small parts of the Rocky Mountains (Mutz and Graham 1982, Cooper and Cottrell 1990).

Methods of riparian vegetation classification vary with the researcher and project goals. The U.S. Forest Service classifies forest ecosystems into "habitat types" based on potential climax vegetation (Daubenmire 1952, Pfister and Arno 1980). Climax vegetation represents the stable, self-perpetuating community predicted on the basis of climate, topography, and soils in the absence of disturbance. Often, however, riparian vegetation never reaches climax due to frequent floods (Campbell and Green 1968). Therefore, some researchers classify vegetation into "community types" according to existing structure and composition without reference to successional stage following disturbance. This approach, however, is not concerned with whether vegetation consists primarily of native or exotic species or has been disturbed by human land uses (e.g., Youngblood et al. 1985b, Padgett et al. 1989). Another classification approach (1) recognizes that climax vegetation is seldom reached due to natural disturbances, but focuses on the more mature successional stages; and (2) emphasizes that classification of "natural vegetation," vegetation that is as free as possible of exotic species and the effects of human land uses, provides essential information for effective biodiversity conservation (Baker 1989). Vegetation types classified using either a habitat type approach or Baker's approach are referred to as "associations."

Even if there is only one association along a river reach, there may be several community types. Riparian community types along a river reach comprise a complex which Winward and Padgett (1989) name on the basis of the most prominent community type plus geographical features describing where it occurs. This spatially complex mosaic of community types creates difficulties for classification, but the diversity of communities is an important component of biodiversity (Hunter 1991).

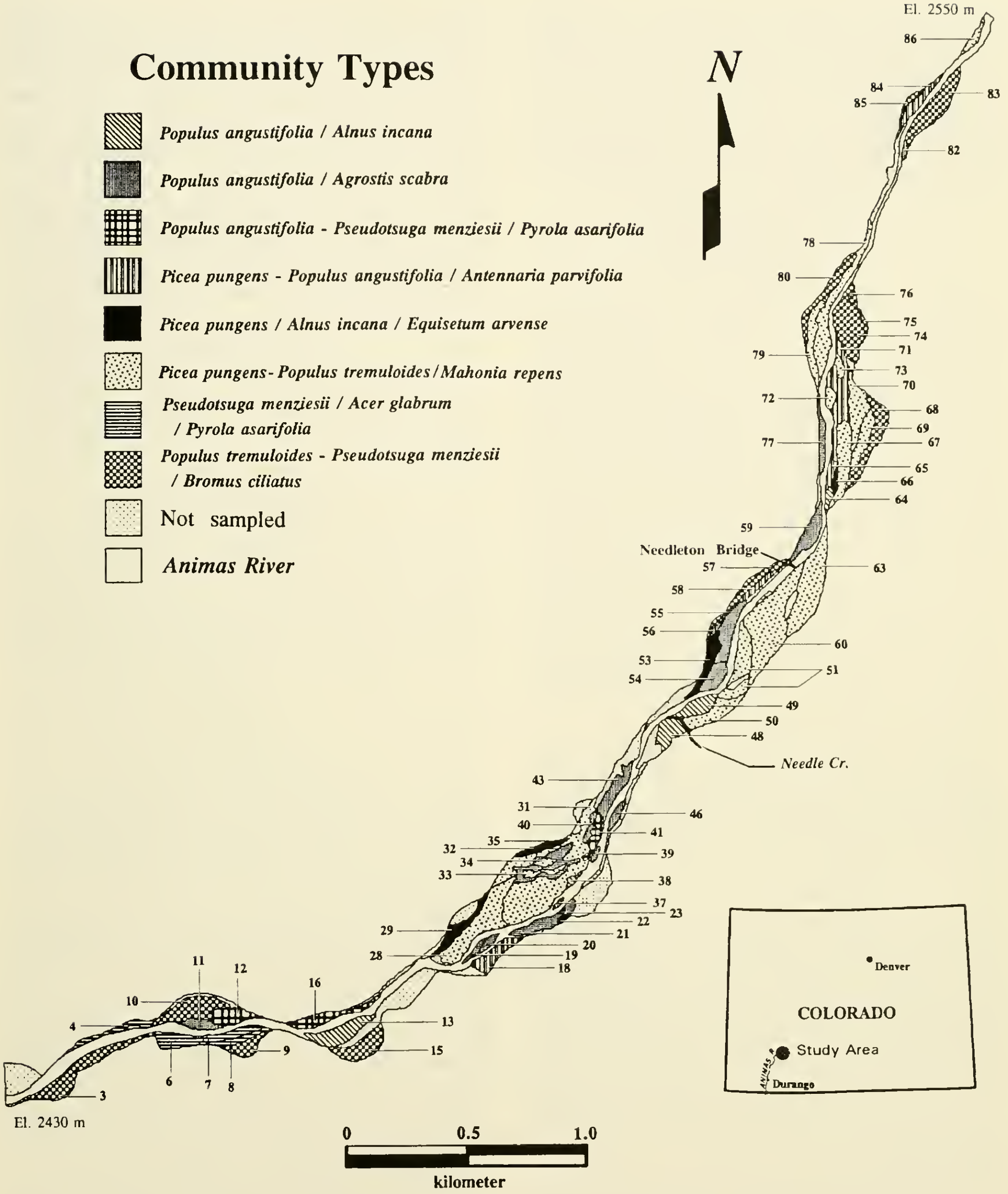
An additional problem is that classification may use only overstory species, or it may be based on the entire flora. Classification traditionally uses one technique or a combination of techniques including subjective grouping, evaluating and sorting of stand tables, cluster analysis, or ordination (Whittaker 1962, Gauch 1982). However, the dominance of the overstory in forests may skew mathematical analyses that use the entire flora (Padgett et al. 1989). In northern regions, where the understory flora often is more sensitive to environmental variation than is the overstory (Whittaker 1962), quantitative techniques that give equal weight to the understory and overstory may not be ideal.

Along the Animas River in southwestern Colorado's San Juan Mountains, we investigated variation in plant species composition of contiguous patches of riparian vegetation. We classified riparian vegetation along a 6-km reach using both understory and overstory vegetation. Goals of this paper are to identify community types found along the river reach, to describe the community types in relation to their environment, and to explain a new approach to balance the use of both overstory and understory vegetation data in quantitative classification. This approach, we suggest, may lead to community classifications more useful for conservation and management.

STUDY AREA

The Animas River starts in the San Juan Mountains of southwestern Colorado and flows south to the San Juan River in New Mexico. The study area is approximately 40 km northeast of Durango in LaPlata County (Fig. 1), along a continuous 6-km reach of the Animas River between 2430 and 2550 m in elevation. This is one of the least disturbed montane river reaches in western Colorado (Baker 1990). A narrow-gauge railroad track and a wilderness access trail occur along the reach, but the reach has probably never been grazed by cattle or sheep. There are some silver and gold mines upstream.

The Animas is an unregulated gravelbed river with a mean annual peak flow of 145 m^3s^{-1}. Within the study reach the river has a mean gradient of 0.0193, a mean channel width of 34.3 m, and a mean channel depth of 3.6 m. The river is entrenched in a deep canyon surrounded by the Needle Mountains. The valley, varying in width from less than 100 m to about 400 m, is lined with alluvial deposits formed from Precambrian granites in the north and south


Community Types
Populus angustifolia / Alnus incana
Populus angustifolia / Agrostis scabra
Populus angustifolia - Pseudotsuga menziesii / Pyrola asarifolia
Picea pungens - Populus angustifolia / Antennaria parvifolia
Picea pungens / Alnus incana / Equisetum arvense
Picea pungens- Populus tremuloides/Mahonia repens
Pseudotsuga menziesii / Acer glabrum / Pyrola asarifolia
Populus tremuloides - Pseudotsuga menziesii / Bromus ciliatus
Not sampled
Animas River
N
El. 2550 m
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El. 2430 m
0
0.5
1.0
kilometer
Denver
COLORADO
Study Area
ANIMAS
Durango

Fig. 1. Animas River study area and its location in Colorado. Patches are shaded according to their community type and numbered for identification.

sections of the study area and from Precambrian gneiss and schist in the central section of the study area (Osterwald 1989).

METHODS

Previous work on the study reach focused on the structure of riparian tree populations in relation to floods and climatic fluctuations (Baker 1988, 1990). Baker (1988) identified 57 vegetation patches having distinct boundaries recognizable on aerial photographs and on the ground. This patchiness is largely the result of tree regeneration after past floods (Baker 1990). In the field we refined the boundaries of some of the 57 patches and identified new patches for a total of 67 patches available for sampling. Patches were mapped on aerial photographs in the field, then digitized and rectified using the GRASS geographic information system (USA-CERL 1991). A final map of patch locations and vegetation (Fig. 1) was produced with ATLAS Draw (Strategic Mapping 1991).

Vegetation Sampling and Environmental Data

Within each of the 67 patches, one 20 × 50-m plot (0.1 ha) was subjectively placed parallel to the river to obtain a representative sample of herbaceous and woody vegetation. Methods of herbaceous vegetation sampling followed Peet (1981). Percent cover of each vascular plant species (except trees) present was estimated, during mid-growing season, in 25 contiguous 0.5 × 2-m quadrats along the 50-m center line of each plot. Percent cover of 0–10% was estimated to the nearest 1%; percent cover of 10–100% was estimated to the nearest 5%. Species located during a survey of the plot, but not found in the quadrats, were assigned 0.1% cover. Nomenclature follows Kartesz and Kartesz (1980).

Baker (1988) collected data on diameter-at-breast-height (dbh) size classes of tree species in his original 57 stands. We added to this data set by tallying trees (>2.5 cm dbh in 10-cm classes), saplings (<2.5 cm dbh and >1 m tall), and seedlings (<2.5 cm dbh and <1 m tall) of each species in plots of the 10 additional patches as Baker had done. Increment cores were extracted from the bases of 5–15 of the largest trees in each patch for estimating patch age. Ages of the largest trees tend to be similar, reflecting a common origin following floods (Baker 1990). Each patch was assigned to a 10-year age class according to the maximum age of the 5–15 cored trees. Age zero is A.D. 1990.

A set of environmental variables was measured in the field in each patch. Patch slope was measured using an Abney level and survey rod. Aspect of the patch was measured in degrees with a compass. We surveyed the distance to the channel and the height above the channel using the rod, level, and a distance meter. Patches were identified as either on terraces or depositional bars. The depositional bar is the lowest prominent feature higher than, but within, the channel bed, while terraces are older, higher fluvial landforms (Osterkamp and Hupp 1984). At every 0.5 m along the 50-m center line of each plot, we measured the intermediate axis of the surface particle at that point and assigned it to a size class, in a variation of the Wolman (1954) technique. Later, using Rodriguez's (1986) MOMENTS program, we calculated mean size, %<1 mm, %<2 mm, and sorting value for each patch. Soil samples of the upper 15 cm of the profile were taken in only 20 of the 67 patches, due to the cost of chemical analyses. These 20 samples spanned the spectrum of patch ages and floristic and environmental variation. Samples were later analyzed for standard fertility (organic matter, pH, N, P, and electrical conductivity) by the University of Wyoming Soil Testing Lab.

Quantitative Analyses

We used the SPSS/PC+ cluster analysis program (SPSS 1990) to determine groups of patches similar in overstory and understory vegetation composition (Romesburg 1984). After experimenting with several clustering methods, we identified the BAVERAGE method (average linkage between groups) and the cosine distance measure (angular separation of vectors of variables) as the best clustering combination. This combination emphasizes relative abundances within a plot and de-emphasizes absolute abundance differences between plots (SPSS 1990).

Species composition data were also ordinated by detrended correspondence analysis (DCA) using CANOCO (Canonical Community Ordination), a multivariate statistical program for applications in community ecology (Ter Braak 1988). Correspondence analysis provides a geometrical representation of the relationships among samples and species in a data set and identifies the dominant trend of variation in community composition.

Initial ordination and cluster analysis of the combined overstory and understory data set resulted in groupings primarily reflecting just the high cover values of overstory tree species rather than the joint pattern of both overstory and understory species. To counteract this, we analyzed the overstory tree species size-class data and the understory shrub and herbaceous species cover data separately, and then merged the two results. The overstory size-class data of each plot were first clustered; then the percent cover data of understory shrubby and herbaceous species in each plot were clustered. These understory cover data were also ordinated using DCA. Final classification groups were the result of intersections of overstory cluster groups with understory cluster groups overlain on the understory DCA ordination diagram. We calculated the mean value for several environmental variables in each community type. Environmental variables we used are those found to be important to vegetational variation along the reach based on a separate, but related, gradient analysis (Baker and Walford 1995).

Classification groups referred to here are "community types" because they represent existing rather than potential natural vegetation. Each community type is based on the entire flora but is named based on the dominant species in the overstory and the dominant or most diagnostic indicator species in the understory (Mueller-Dombois and Ellenberg 1974). When there are co-dominants in a layer, both species are included in the name and are separated by a hyphen.

RESULTS

Classification

The cluster analysis and DCA ordination of the plot understory cover data (grasses, forbs, and shrubs) suggested four major groups and one outlier (Fig. 2). The similarity cut level was kept coarse so that overstory cluster groups could be incorporated later. This specific level was chosen after considering alternative cut levels at slightly greater or lesser similarity (Fig. 2). Groups A and B, for example, would become one group if the cut level were at a slightly lower similarity, yet these two groups are quite different (Fig. 2). Ordination of the same data set is represented by the DCA Axis 1 vs. Axis 2 ordination diagram (Fig. 3a). The distinctiveness of understory groups produced by cluster analysis is supported by the comparatively distinct location of the groups on this ordination diagram.

Understory groups identified by cluster analysis and ordination are compositionally distinct and occur in different environmental settings. Group A was dominated by *Alnus incana* and *Equisetum arvense*. These patches were predominantly located on bars. Group B was located entirely on bars and had the fewest species of any group. *Agrostis scabra* was always present in Group B patches. The third group (C) was dominated by *Rosa woodsii* and *Pyrola asarifolia*. Patches of Group D are almost always on terraces and generally have the highest species richness. *Mahonia repens* is always present, and *Rosa woodsii*, *Bromus ciliatus*, and *Oryzopsis asperifolia* are usually well represented.

Overstory size-class data were clustered by the same method. Three overstory groups were identified at approximately 25% similarity (Fig. 4). Each of these major groups has members from at least three different understory groups. Group I is recognized by a dominance of *Populus angustifolia* seedlings, saplings, and small trees (Table 1). All understory Group B members are found within this overstory group. But other members of this overstory group have the understory of Groups A, C, D, or E. Overstory Group II is characterized by *Picea pungens* of all sizes and larger *P. angustifolia*

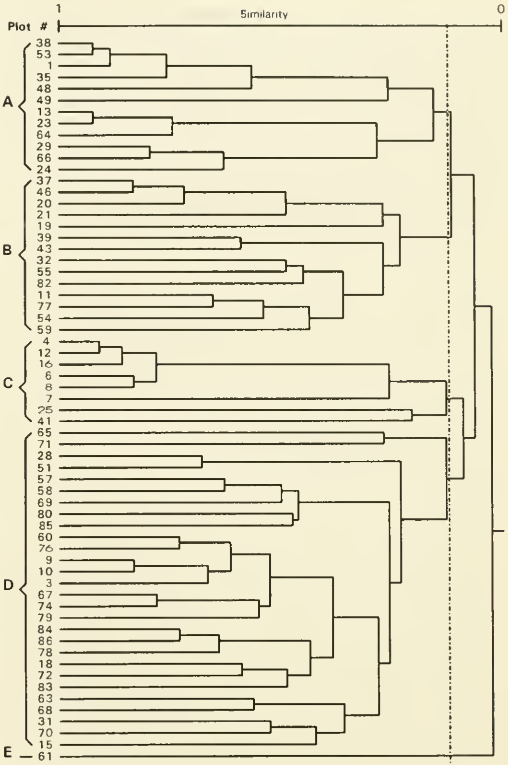

Fig. 2. Understory cluster analysis dendrogram based on percent cover of herbaceous and shrubby species. Plot numbers correspond with patch numbers on the study area map (see Fig. 1). The dashed line indicates the similarity level at which understory groups were separated.

(Table 1). Most of its members have an understory of Groups A or D. The third overstory group tends to have a mixed canopy dominated by all sizes of *Pseudotsuga menziesii* and small *Abies concolor* (Table 1). *Populus tremuloides* and *Picea pungens* are often present. Half of the members of understory Groups C and D have this mixed overstory composition.

These overstory groups are indicated on the same DCA ordination diagram (Fig. 3b). Since this diagram represents the ordination of shrubby and herbaceous species in plots, and the understory composition varies within the overstory groups, it is not surprising that these overstory cluster groups are scattered within the ordination diagram. This suggests that the understory is to some extent independent of the overstory.

Final classification groups resulted from the intersection of the understory groups and overstory groups overlain on the ordination diagram (Fig. 3c). This results in eight final classification groups plus two single-member groups and one outlier plot. The symbol for each classification group is a combination of its overstory cluster group (I, II, or III; Fig. 4) and its understory cluster group (A, B, C, or D; Fig. 2). Groups are presented in an age sequence within their overstory group, from youngest (IB) to oldest (IIID).

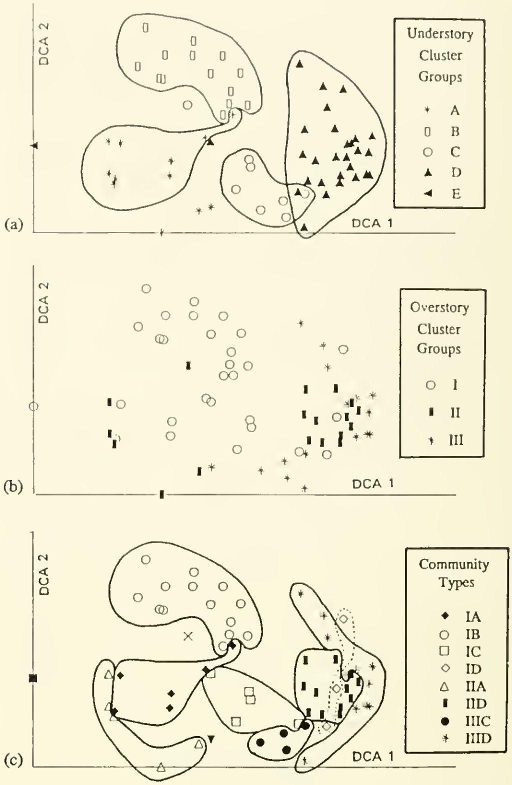

Fig. 3. Ordination diagrams obtained by detrended correspondence analysis of data on percent cover of shrubby and herbaceous species in the plots: (a) plots are coded according to their understory cluster analysis group (see Fig. 2); (b) plots are coded according to their overstory cluster analysis group (see Fig. 4); (c) plots are coded according to their final community type, based on the intersection of understory cluster groups with overstory cluster groups.

Community Types

The following paragraphs summarize tree composition and structure, understory species composition, and environment of each of the eight community types (Tables 1, 2). In prior analyses (Baker and Walford 1995) the gradient controlling spatial variation of the shrubby and herbaceous vegetation mosaic was found to be age and disturbance related. Variables most affected by disturbance events are illustrated for each community type (Fig. 5). A map of the patches and their community type is in Figure 1.

[IB] *Populus angustifolia / Agrostis scabra.*—The 14 patches constituting this community type are found on bars close to the channel in both height and distance (Fig. 5). Of the eight major types, this type was most recently established (mean age = 31 years) and has the largest mean surficial sediment size. Its soils have low organic matter. Patches of this type are most common in the middle parts of the study reach (Fig. 1). This type is characterized by an abundance of *P. angustifolia* seedlings and saplings (Table 1) and sometimes small to medium-size trees. *Picea pungens* seedlings are almost always present and are sometimes abundant along with saplings and small trees. Small *Pseudotsuga menziesii* and *Abies concolor* may be present. Herbaceous vegetation is very sparse (Table 2). Graminoids dominate the understory with both *Agrostis scabra* and either *Trisetem montanum* or *T. spicatum* always present. *Epilobium latifolium* often occurs in significant amounts.

[IA] *Populus angustifolia / Alnus incana.*—Patches of this type are on average 10 years older than those of Type IB (Fig. 5). This community type is found on bars slightly higher above the channel than those of IB. Surface sediment sizes are diverse, but soils have little organic matter. Like Type IB, these patches

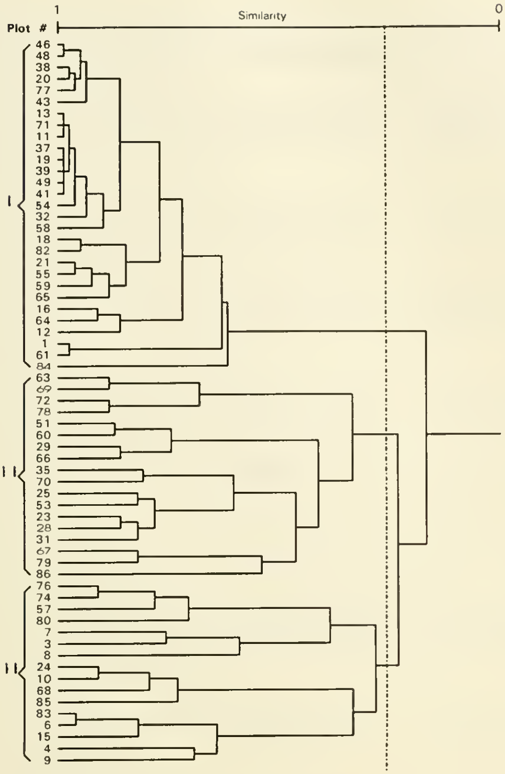

Fig. 4. Overstory cluster analysis dendrogram based on size-class data of tree species. Plot numbers correspond with patch numbers on the study area map (see Fig 1). The dashed line indicates the similarity level at which overstory groups were separated.

are most common in the middle part of the study reach (Fig. 1). *Populus angustifolia* characterizes stands of this type; many small and some medium-size trees are present along with abundant seedlings and saplings (Table 1). *Picea pungens* and *Pseudotsuga menziesii* seedlings and saplings are usually present. The understory composition distinguishes this type from IB (Table 2). Shrubs are more common. *Alnus incana* is always present and *Salix drummondiana* is usually present. *Agrostis scabra* is occasionally present in minor amounts.

[IC] *Populus angustifolia–Pseudotsuga menziesii / Pyrola asarifolia.*—This small community type comprises two patches on bars and one on a terrace, with an average surface particle size <10 mm and soils with low organic matter (Fig. 5). Patches in this community type are scattered along the study reach (Fig. 1). The largest trees and most abundant seedlings of this type are *P. angustifolia* (Table 1). *Pseudotsuga menziesii* are always present as seedlings through medium-size trees. Medium-size *Picea pungens* or *Abies concolor* may also be present. *Pinus strobiformis* seedlings or saplings are always present in this type. The understory of this type is not dense, and all but one of the understory species have cover values <0.8% (Table 2). Three shrub species occur in small amounts. *Pyrola asarifolia* is always present in the highest amount of any understory species.

[ID] *Picea pungens–Populus angustifolia / Antennaria parvifolia.*—Three terrace patches and two patches on bars make up this community type, which occurs on surfaces <1 m above the channel that have soils with low organic matter content (Fig. 5). Patches in this type are scattered along the study reach (Fig. 1). They have strong similarities in overstory composition and weak ones in understory composition. *Picea pungens* and *P. angustifolia* are the largest trees of this type and are always present as seedlings, saplings, and small trees (Table 1). *Abies concolor* and *Pseudotsuga menziesii* seedlings can always be found. The lack of a constant understory is reflected in the low similarity level at which patches 65 and 71 are joined in the dendrogram (Fig. 2). Six species are present at 80% constancy, *Antennaria parvifolia* having the greatest mean cover in the type. No single herbaceous or shrubby species is present in all five patches of this type, but in general there is much more herbaceous and shrubby vegetation present than in types IA, IB, and IC (Table 2).

[IIA] *Picea pungens / Alnus incana / Equisetum arvense.*—Patches of this community type occur in more persistently moist areas. They span several age classes, can be found on bars or terraces, and have developed finer surficial sediments than might be expected for their age class (Fig. 5). Their soils typically contain only a little more organic matter than soils in patches of Type I. Patches in this type are scattered along the study reach (Fig. 1). *Picea pungens* seedlings, saplings, and small to medium-size trees as well as *P. angustifolia* of various sizes characterize the type (Table 1). Few other tree species occur, although *Pseudotsuga menziesii* may be present in small amounts. *Alnus incana* and *Salix drummondiana* are the dominant shrubs of this type, both occurring in greater amounts here than in any other types (Table 2). *Equisetum arvense* is always present in substantial amounts. Sedges

TABLE 1. Mean overstory stem density (no. stems per 0.1 ha) and percent constancy by species and size class within community types.

	Community type															
	IB		IA		IC		ID		IIA		IID		IIIC		IIID	
	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %
Abies concolor (Gord. & Glend.) Lindl. ex Hildebr.																
seedling	4.6	50	7.5	33	1.0	33	17.6	100	2.0	20	11.8	83	162.0	75	77.5	100
sapling	1.7	14	0.8	33	0.7	33	3.0	80	1.2	20	5.6	67	32.0	50	11.5	91
3-13 cm	0.1	7	0.0	0	0.0	0	5.6	40	0.0	0	7.1	67	44.0	50	9.1	73
13-23 cm	0.0	0	0.0	0	0.0	0	4.6	80	0.4	20	2.4	50	10.0	75	3.0	55
23-33 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.8	25	4.0	75	1.5	36
33-43 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.2	8	4.3	50	0.8	27
>43 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.4	20	0.6	17	6.0	50	0.6	18
Picea pungens Engelm.																
seedling	37.9	86	25.7	67	7.0	67	42.8	100	91.6	100	19.0	100	4.8	50	11.6	73
sapling	8.1	64	7.5	50	1.3	67	14.2	100	44.2	100	13.3	92	0.3	25	4.1	82
3-13 cm	8.1	50	5.7	50	1.3	67	21.0	100	27.4	100	27.7	100	2.3	50	2.3	55
13-23 cm	0.6	21	1.0	33	1.3	67	5.8	80	9.6	60	9.2	83	0.3	25	1.8	55
23-33 cm	0.0	0	0.0	0	1.7	33	4.4	60	2.4	40	3.3	75	0.3	25	0.4	18
33-43 cm	0.0	0	0.0	0	0.0	0	3.0	60	0.0	0	1.8	50	0.3	25	1.1	36
>43 cm	0.0	0	0.0	0	0.0	0	2.2	40	0.4	20	1.3	42	0.0	0	0.5	27
Pinus ponderosa Laws.																
seedling	1.7	36	0.0	0	1.7	33	0.0	0	0.0	0	0.0	0	0.3	25	0.2	9
sapling	0.0	0	0.2	17	0.0	0	0.0	0	0.0	0	0.0	0	0.3	25	0.1	9
3-13 cm	0.2	14	0.7	17	2.0	33	0.0	0	0.0	0	0.4	17	0.5	25	0.0	0
13-23 cm	0.0	0	0.7	17	2.3	33	0.4	20	0.0	0	0.6	17	0.3	25	0.1	9
23-33 cm	0.0	0	0.3	17	0.3	33	0.2	20	0.0	0	0.2	8	0.0	0	0.2	18
33-43 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.1	9
>43 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.1	9

TABLE 1. Continued.

	Community type															
	IB		IA		IC		ID		IIA		IID		IIIC		IIID	
	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %
Populus angustifolia James																
seedling	175.1	100	251.0	100	67.3	100	184.8	100	20.4	60	5.2	50	2.8	50	0.5	18
sapling	48.5	100	72.7	100	12.7	67	13.0	100	19.0	60	5.7	50	4.0	50	0.5	27
3-13 cm	20.5	79	51.2	100	14.7	100	14.4	60	7.8	60	7.8	67	3.8	50	1.8	27
13-23 cm	6.6	43	7.0	83	7.3	100	7.0	60	6.6	60	6.3	75	3.8	100	7.5	45
23-33 cm	1.5	14	1.8	33	7.0	100	3.6	60	5.0	60	7.1	58	7.5	100	5.6	36
33-43 cm	0.1	7	0.0	0	2.7	67	4.6	40	2.2	80	4.1	58	3.8	75	3.2	36
>43 cm	0.0	0	0.0	0	2.7	67	4.4	40	2.0	20	2.0	25	5.0	75	1.4	18
Populus tremuloides Michx.																
seedling	1.4	21	0.0	0	2.0	67	3.4	40	0.2	20	10.9	83	9.3	50	28.8	73
sapling	0.1	7	0.0	0	2.3	67	1.0	40	0.0	0	24.1	83	2.8	50	5.6	82
3-13 cm	0.0	0	0.0	0	0.0	0	4.0	40	0.0	0	8.8	92	0.3	25	10.1	100
13-23 cm	0.0	0	0.0	0	0.0	0	4.4	40	0.0	0	6.3	75	7.0	25	21.2	91
23-33 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	1.8	42	2.8	50	7.2	73
33-43 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.8	25	1.3	50	0.6	36
>43 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.1	8	0.0	0	0.2	9
Pseudotsuga menziesii (Mirbel) Franco																
seedling	9.5	86	30.8	67	18.0	100	13.6	100	2.4	80	7.4	83	21.0	100	26.0	82
sapling	2.4	50	4.8	33	4.0	100	4.6	80	2.8	60	6.1	75	12.0	100	12.0	91
3-13 cm	1.9	36	5.2	33	7.7	100	12.0	80	4.4	60	4.8	75	22.3	100	12.6	91
13-23 cm	0.0	0	3.2	33	5.0	100	4.0	40	1.6	20	0.9	33	15.8	100	3.5	64
23-33 cm	0.0	0	0.3	17	3.0	100	2.6	40	1.2	40	0.5	25	7.8	75	2.0	27
33-43 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.3	17	1.0	50	2.3	64
>43 cm	0.0	0	0.0	0	0.0	0	0.6	20	0.0	0	0.1	8	1.3	50	0.5	36

TABLE 2. Mean percent cover values for main species in community types (includes species with at least 1% cover in any plot). Species with double underlined cover values had 100% constancy in that community type. Species with single underlined cover values had >80% and <100% constancy in that community type.

	Community type							
	IB	IA	IC	ID	IIA	IID	IIIC	IIID
SHRUBS								
Acer glabrum Torr.	—	—	—	1.7	—	0.2	3.6	1.0
Alnus incana (L.) Moench ssp. *tenuifolia* (Nutt.) Breitung	0.1	0.8	—	0.1	5.0	—	5.1	—
Amelanchier alnifolia (Nutt.) Nutt.	—	—	0.1	0.6	—	0.6	1.0	1.2
Cornus sericea L.	—	—	—	—	—	—	2.4	—
Juniperus communis L.	—	—	0.1	2.3	—	3.9	0.4	2.7
Lonicera involucrata (Richars.) Banks ex Spreng.	—	—	0.1	0.1	0.1	0.4	0.2	—
Mahonia repens (Lindl.) G. Don	—	—	—	1.3	—	4.0	0.3	3.5
Prunus virginiana L.	—	—	—	—	—	1.6	1.4	0.5
Rosa woodsii Lindl.	—	—	0.1	2.1	—	1.8	1.5	3.1
Rubus parviflorus Nutt.	—	0.1	—	—	—	—	0.8	—
Rubus strigosus Michx.	—	—	—	0.4	0.1	0.2	0.4	0.5
Salix drummondiana Barratt ex Hook.	0.1	0.8	—	—	11.3	—	—	—
Salix lasiandra Benth.	—	0.4	—	—	—	—	—	—
FORBS								
Achillea millefolium L. var. *lanulosa* (Nutt.) Piper	—	0.2	—	0.9	0.1	1.0	—	0.8
Anaphalis margaritaceae (L.) Benth. & Hook. f. ex C. B. Clarke	—	—	—	—	0.3	0.1	0.1	—
Antennaria parvifolia Nutt.	—	—	0.1	2.9	—	1.2	—	4.0
Apocynum androsaemifolium L.	—	—	—	0.1	—	—	—	1.8
Arabis divaricarpa A. Nels.	0.1	—	0.3	—	—	—	—	—
Arabis hirsuta (L.) Scop.	0.1	—	—	—	—	—	—	—
Arctostaphylos uva-ursi (L.) Spreng.	—	—	—	—	0.1	—	0.9	0.2
Arnica cordifolia Hook.	—	—	—	—	—	—	0.7	—
Artemisia carruthii Wood ex Carruthers	—	—	—	0.3	—	—	—	0.1
Artemisia franserioides Greene	—	—	—	1.4	—	1.8	1.3	4.5
Artemisia ludoviciana Nutt.	—	—	—	0.8	—	0.1	—	0.2
Cerastium fontanum Baumg.	—	—	—	—	0.3	0.2	—	0.3
Epilobium angustifolium L.	—	—	0.3	0.3	0.1	0.5	0.2	0.3
Epilobium latifolium L.	0.7	0.1	—	—	—	—	—	—
Equisetum arvense L.	0.1	0.1	—	—	16.8	—	0.4	0.1
Erigeron eximius Greene	—	—	—	0.3	—	1.3	—	4.5
Erigeron flagellaris Gray	—	—	—	0.2	—	0.5	—	0.5
Erigeron formosisimus Greene	—	—	—	3.0	—	1.3	—	2.4
Erigeron speciosus (Lindl.) DC. var. *speciosus*	—	—	—	—	—	0.1	1.8	—

TABLE 2. Continued.

	Community type							
	IB	IA	IC	ID	IIA	IID	IIIC	IIID
Fragaria vesca L. ssp. *americana* (Porter) Staudt	—	—	—	0.8	—	1.5	0.1	0.9
Fragaria virginiana Duchesne	—	—	—	0.3	—	0.6	—	1.4
Galium triflorum Michx.	—	—	0.1	0.7	0.1	0.2	2.6	0.6
Geranium richardsonii Fisch. & Trautv.	—	—	—	2.0	0.1	2.2	2.4	3.4
Haplopappus parryi Gray	—	—	—	2.4	—	2.1	1.5	1.5
Heracleum lanatum Michx.	—	—	—	1.0	—	0.2	2.2	3.6
Humulus lupulus L. var. *lupuloides* E. Small	—	—	—	—	—	—	—	0.1
Lathyrus brachycalyx Rydb.	—	—	—	—	—	—	—	0.3
Ligusticum porteri Coult. & Rose	—	—	—	—	—	—	0.7	0.1
Lithospermum multiflorum Torr. ex Gray	—	—	—	0.7	—	0.4	0.1	1.3
Mertensia franciscana Heller	—	—	—	0.2	—	0.2	1.1	0.9
Orthilia secunda (L.) House	—	—	0.1	—	—	0.1	1.1	0.2
Osmorhiza chilensis Hook. & Arn.	—	—	—	—	—	—	3.2	0.1
Osmorhiza depauperata Phil.	—	—	—	1.2	—	0.1	1.6	0.5
Oxytropis deflexa (Pallas) DC. var. *sericea* Torr. & Gray	—	—	—	1.3	—	0.1	—	0.2
Platanthera hyperborea (L.) Lindl. var. *hyperborea*	—	—	—	—	0.4	—	—	—
Potentilla hippiana Lehm.	—	—	—	1.0	—	0.3	—	0.8
Pseudocymopterus montanus (Gray) Coult. & Rose	—	0.1	—	1.4	—	0.6	0.1	0.4
Pteridium aquilinum (L.) Kuhn	—	—	—	—	—	—	—	0.1
Pyrola asarifolia Michx.	—	—	2.0	0.4	0.5	0.6	18.3	0.4
Rudbeckia laciniata L.	—	—	—	—	—	0.3	4.0	1.6
Senecio fendleri Gray	0.2	—	0.1	0.3	0.1	0.2	0.4	0.3
Silene menziesii Hook.	0.1	0.1	0.1	0.2	0.3	0.4	0.3	0.2
Smilacina stellata (L.) Desf.	—	—	0.1	5.1	—	3.8	1.7	2.3
Solidago canadensis L. var. *salebrosa* (Piper) M. E. Jones	—	—	0.1	0.1	—	0.1	0.1	0.2
Thalictrum fendleri Engelm. ex Gray	—	—	—	1.1	—	5.1	0.3	4.8
Thlaspi montanum L.	0.1	0.1	0.1	—	0.1	—	—	—
Urtica dioica L.	—	—	—	—	—	—	—	0.2
Vicia americana Muhl. ex Willd.	—	—	—	0.2	—	0.5	0.1	1.0
Viola canadensis L.	—	—	—	0.3	—	0.6	2.1	0.7
Viola nephrophylla Greene	—	—	—	—	—	0.3	0.1	—
GRAMINOIDS								
Agropyron trachycaulum (Link) Malte ex H.F. Lewis var. *trachycaulum*	—	—	—	—	—	0.4	—	0.2
Agropyron trachycaulum (Link) Malte ex H.F. Lewis var. *unilaterale* (Vasey) Malte	—	—	—	0.1	—	—	—	0.4

TABLE 2. Continued.

	Community type							
	IB	IA	IC	ID	IIA	IID	IIIC	IIID
Agrostis scabra Willd.	0.3	0.1	0.1	—	1.8	—	0.1	—
Agrostis stolonifera L. var. *stolonifera*	—	—	—	—	0.9	—	—	—
Blepharoneuron tricholepis (Torr.) Nash	—	—	—	1.2	—	—	—	0.4
Bromus anomalus Rurp. ex Fourn.	—	—	—	—	—	—	—	0.2
Bromus ciliatus L.	—	—	0.1	1.7	—	1.6	1.1	4.0
Calamagrostis canadensis (Michx.) Beauv.	—	—	0.2	—	0.1	1.3	0.6	0.7
Carex foenea Willd.	—	—	—	1.1	—	3.3	0.8	2.0
Carex kelloggii W. Boott ex S. Wats.	—	—	—	—	3.6	—	—	—
Carex pityophila Mackenzie	—	—	—	0.3	0.2	0.2	0.1	0.1
Carex rossii Boott ex Hook.	0.1	—	0.3	0.6	0.1	—	—	0.3
Deschampsia cespitosa (L.) Beauv.	0.5	0.1	—	—	1.1	—	—	—
Elymus glaucus Buckl.	—	—	—	—	—	0.1	0.4	0.6
Festuca thurberi Vasey	—	—	—	—	—	—	—	0.3
Juncus balticus Willd.	—	—	—	—	7.2	—	—	0.3
Juncus saximontanus A. Nels.	—	—	—	—	1.0	—	—	—
Juncus tenuis Willd. var. *uniflorus* (Farw.) Farw.	—	—	—	0.5	—	—	—	—
Koeleria cristata (L.) Pers.	—	—	—	—	—	0.1	—	0.6
Muhlenbergia richardsonis (Trin.) Rydb.	—	—	—	—	—	—	—	0.1
Oryzopsis asperifolia Michx.	0.1	—	—	1.3	—	1.7	3.6	6.2
Poa palustris L.	0.1	0.1	—	—	2.3	0.1	0.1	0.2
Schizachne purpurascens (Torr.) Swallen	—	—	—	—	—	0.2	—	0.1
Sitanion hystrix (Nutt.) J. G. Sm.	—	—	—	0.1	—	0.1	—	0.6
Stipa columbiana Macoun	—	—	—	—	—	0.1	—	0.2
Trisetum montanum Vasey	0.4	0.1	0.1	—	0.8	—	—	—
Trisetum spicatum (L.) Richter	0.1	—	0.1	0.1	—	—	—	—
EXOTICS								
Poa pratensis L.	0.8	—	—	1.2	—	2.8	0.1	3.7
Poa trivialis L.	—	—	—	—	2.3	—	—	—
Taraxacum officinale Weber	0.1	0.1	—	0.6	0.1	1.4	0.1	0.5

and rushes dominate the graminoid layer, with *Juncus balticus* always present.

[IID] *Picea pungens–Populus tremuloides / Mahonia repens.*—Ages of these patches span the range from 40 to 130 years. Most are found on terraces, with 89% of their surficial sediment <1 mm in size (Fig. 5). Soils in this type contain moderate amounts of organic matter (Fig. 5). Patches in this community type are most common in the upper two-thirds of the study reach (Fig. 1). This type is characterized by *P. tremuloides* and *P. pungens* of all sizes (Table 1). *Populus angustifolia* is not regenerating strongly but is sometimes the largest tree in a patch. *Abies concolor* and *Pseudotsuga menziesii* may also be present, usually in small sizes. *Mahonia repens, Juniperus communis,* and *Rosa woodsii* are dominant shrubs (Table 2); *Thalictrum fendleri* and *Smilacina stellata* are dominant forbs. The graminoid layer is characterized by *Bromus ciliatus*, with significant amounts of *Carex foenea* often present.

[IIIC] *Pseudotsuga menziesii / Acer glabrum / Pyrola asarifolia.*—The four patches of this community type are all found on terraces with fine surface sediments, have about the same

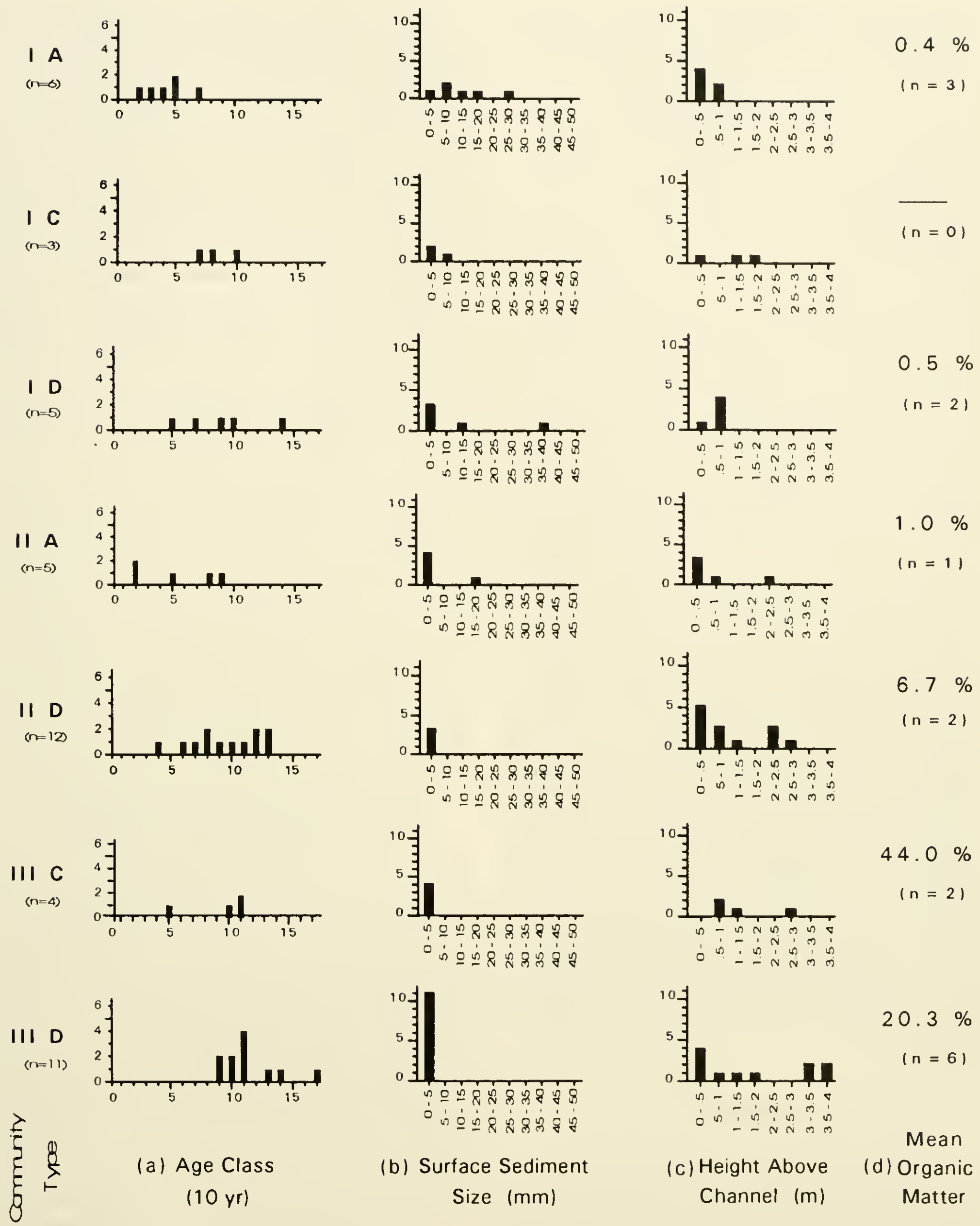

Fig. 5. Environmental attributes within each community type (see Fig. 1). Histograms (a–c) show the frequency on the vertical axis.

age-class span as patches in Type IID, and have the largest mean organic matter content of community types along the reach (Fig. 5). The overstory is a mixed forest similar to Type IIID, but the understory is not as rich. Patches in this type are restricted to the lower one-third of the study reach (Fig. 1). *Pseudotsuga menziesii*, *Populus angustifolia*, and usually *Abies concolor* are the large trees of these patches (Table 1). *Populus angustifolia* seedlings or saplings are rare. Regeneration appears strongest in *Abies concolor* and *P. menziesii* (Table 1). *Acer glabrum* is the dominant shrub usually associated with lesser amounts of *Alnus* *incana*, *Prunus virginiana*, and *Rosa woodsii* (Table 2). *Pyrola asarifolia* is the most prevalent forb with cover values averaging 18%. *Geranium richardsonii*, *Smilacina stellata*, *Haplopappus parryi*, and *Artemisia franserioides* always occur. *Oryzopsis asperifolia* is the dominant graminoid, with *Bromus ciliatus* in lesser amounts.

[IIID] *Populus tremuloides–Pseudotsuga menziesii / Bromus ciliatus*.—Examples of this community type are found on terraces an average of 1.75 m above the channel (Fig. 5). Surface particles are predominantly <1 mm, while soils have about 20% organic matter content (Fig. 5). The 11 patches comprising this type have the oldest average age and are most common in the lower one-third and upper one-third of the study reach (Fig. 1). This group of patches is a mixed forest type, with the densest understory of all the types. *Populus tremuloides* and *P. menziesii* tend to be the largest and the most abundant trees of these patches. Some patches have very large *Populus angustifolia* as well. *Abies concolor* seedlings and saplings are always present, sometimes in very large numbers. A few *Picea pungens* of various sizes usually can be found. *Mahonia repens*, *Rosa woodsii*, and *Juniperus communis* are co-dominant shrubs. Five *Erigeron* species were found in the 11 patches of this type, with one to three species present in each patch. *Antennaria parvifolia* and *Geranium richardsonii* had high cover values in most patches. Dominant grasses were *Bromus ciliatus* and *Oryzopsis asperifolia*, their quantities being distinctive from any other type.

DISCUSSION

The New Classification Technique

Ecologists working in northern climates have long recognized that individual stratal layers (e.g., tree and shrub) or "synusia" within forest communities may be distributed somewhat independently and may not all have the same value in distinguishing vegetation units (Whittaker 1962). Classification approaches of the northern European schools, such as the "sociations" of the Uppsala school and "site-types" of Cajander (Whittaker 1962), emphasize that lower strata often are more useful in classification, although the tree layer is of some importance as well.

Yet, common multivariate techniques for analyzing vegetation data ignore the synusial affiliations of the species in a community (e.g., Gauch 1982). Since cover values of overstory tree species are often large relative to cover values of understory species, overstory species may prevent understory species from having much influence on the outcome of multivariate analyses (e.g., Padgett et al. 1989). Moreover, these techniques do not take advantage of the different kinds of data that are useful in describing the structure of different synusia. For example, it is much easier and more useful to obtain size-class structure data than cover data for overstory trees in forests, as size-class data can indicate tree composition and abundance as well as population structure (e.g., regeneration status). The value of both kinds of data in forests has long been recognized (e.g., Pfister et al. 1977). Yet, size-class data and cover data are incompatible and cannot both be used readily in a single multivariate analysis. The technique used here allows an equal consideration of both the understory and overstory data and data of different types from different synusia. Community types that are produced have homogeneous tree populations combined with homogeneous understories.

Community types identified using this technique can be useful in conservation and management. The eight community types reflect major variations in vegetation and environment along the reach. A preserve could be designed, shorter than the full length of the reach, that contained all eight community types; it is likely that much of the floristic variation along the reach would then be protected. Moreover, the community types should be useful in management because they are (1) functionally homogeneous, in the sense that tree populations within a type might respond similarly to disturbances, and (2) environmentally sensitive, in the sense that the finer environmental discrimination of understory synusia common in northern regions has been incorporated.

The Community Types in a Regional Context

Community types identified in this study have not been widely reported. This is probably due to the river-reach scale of the study and the tendency to exclude very young vegetation in developing regional classifications. This is also one of a very few river systems in the southern Rocky Mountains with a complete mosaic of riparian vegetation relatively free from human land uses; thus, there have been few other opportunities for this kind of study.

Our Type IIIC is very similar to Baker's (1989) *Abies concolor–Picea pungens–Populus angustifolia / Acer glabrum* association, previously found along the Animas River and the San Juan River, as well as in northern New Mexico (DeVelice et al. 1986). Baker collected data from within the study reach, which explains the similarity of his association with our Type IIIC, but his goal was to classify vegetation regionally based upon the similarity of the more mature vegetation patches along separate rivers. Baker did not sample the mature stands containing *Populus tremuloides* that are found in our Type IID and IIID, thinking they were earlier successional stages of our Type IIIC. However, the age-class data (Fig. 5) suggest that stands within Types IID and IIID are just as old as or older than those in Type IIIC. Thus, although it may be a necessary shortcut for regional classification efforts, sampling and classifying only the mature vegetation may result in errors if the successional sequence along a reach is not clearly understood.

Sampling and Classification of Riparian Vegetation Complexes

In riparian areas, and perhaps anywhere vegetation classification is being approached, it is important to sample and classify not only mature vegetation stands but younger stands as well. The diverse patch structure along rivers may only reach a homogeneous mature composition similar to that in the older patches if the fluvial disturbances that have produced the mosaic are controlled. Moreover, younger stands may not all be leading to the same mature community; there may instead be more than one seral sequence.

This spatial and temporal complexity at the river-reach scale compounds the difficulty of developing regional classifications. One solution to this problem is to adjust the scale of sampling to the scale of patchiness produced by the primary ecological processes (e.g., fires, floods) in a particular landscape. An area such as this free-flowing river requires fine-scale sampling as there is a fine-scale mosaic produced by disturbances and geomorphic variation. A river with less geomorphic complexity or a coarser, more infrequent flood-produced patchiness may require only a coarse sampling focused on the more mature vegetation.

Spatial Variation in Vegetation Along the Reach

The sampling and vegetation analysis suggest that substantial landscape diversity is produced by floods and geomorphic variation along this reach of the Animas River (Fig. 1). The spatial arrangement of this diversity is controlled in part by location of tributaries and width of the valley floor, both of which influence how and where floods create new patches. Needle Creek flows into the Animas River in approximately the middle of the study reach (Fig. 1). Smaller tributaries enter above and below this point, but none carries as great a volume of water. The valley floor also widens approximately 0.5 km below the entry of Needle Creek.

The first four community types (IA, IB, IC, and ID) with *Populus angustifolia* in their overstory are found primarily in this section at the outer river curves or mid-channel where scouring is greatest. The wet environment IIA patches also are found in this wider section, often away from the main channel on side channels that dissect major patches. None of the largest trees is found in this middle section of the reach. In contrast, community types with a more mature overstory are more common in the lower one-third and upper one-third of the study reach. These parts are narrower and have fewer substantial tributaries. Many of the mature vegetation patches are located on terraces quite high above the channel in these parts of the reach.

CONCLUSIONS

This study of riparian vegetation on the river-reach scale revealed considerable spatial and temporal complexity. Flood disturbances, modulated by variation in valley morphology and tributary location, have created distinct patchiness in the vegetation. A new technique, based on both overstory and understory species, offers an improved quantitative method for identifying community types. If classification is to be used effectively to aid in conservation, greater attention to younger, less mature stands of vegetation may be needed. These young stands are a major component of the biodiversity on the river-reach scale and can represent seral stages of new vegetation associations unlike the association represented by present mature stands. Spatial complexity along a single river may make the development of regional classifications, based on many rivers, more difficult. However, regional classifications can still be completed, and will be more valuable, if sampling efforts are tuned to the scale of patchiness and complexity along river reaches.

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ADDITIONS TO KNOWLEDGE OF PALEOCENE MAMMALS FROM THE NORTH HORN FORMATION, CENTRAL UTAH

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ABSTRACT.—The distinctive but inadequately known Paleocene faunas of central Utah are significant in that they sample a time interval not well represented by sequences in other areas. New materials from the Wagon Road (late Puercan) and Dragon (early Torrejonian) local faunas, North Horn Formation, provide additional information on the composition of the assemblages and systematics of included mammal taxa. The proteutherian ?*Propalaeosinopa* is recorded, for the first time, from the Wagon Road fauna, indicating a significant extension for the enigmatic family Pantolestidae, otherwise first known from the Torrejonian. Associated premolars of *Aphronorus simpsoni*, a pentacodontid proteutherian from the Dragon fauna, indicate that the species is more distinct from its Torrejonian congener, *A. fraudator*, than previously suspected. New materials of *Desmatoclaenus hermaeus* uphold the synonymy of this species with *D. paracreodus* and permit more adequate definition of the genus with respect to the arctocyonid *Loxolophus* and the phenacodontid *Tetraclaenodon*; because *Desmatoclaenus* appears to share derived morphology with *Loxolophus*, we refer it to the basal condylarth family Arctocyonidae. The periptychid condylarth *Haploconus*, represented in the Wagon Road fauna by the geologically oldest described species of the genus, *H. elachistus*, is shown to be distinctive in the configuration of lower molars and premolars; *H. elachistus* appears to be more primitive than species known from the Torrejonian of New Mexico. Some features of *Haploconus* are suggestive of the Conacodontinae, a distinctive clade of diminutive periptychids.

Key words: Paleocene, North Horn Formation, Puercan, Torrejonian, Dragon local fauna, Wagon Road local fauna, Mammalia.

Paleocene mammals were first reported from the North Horn Formation, Emery and Sanpete counties, UT, by Gazin (1938). Further fieldwork resulted in the recovery of additional taxa, interpreted as representing two faunas, from two main localities (Gazin 1939, 1941). In subsequent years, additional sites in the region have yielded further specimens, including more taxa and a third faunal assemblage (Spieker 1960, Van Valen 1978, Tomida and Butler 1980, Tomida 1982, Robison 1986, Archibald, Rigby, and Robison 1983). Three assemblages are currently recognized, the Gas Tank, Wagon Road, and Dragon local faunas (Robison 1986). On the basis of the latter two, a "Dragonian" land-mammal age was initially established (Wood et al. 1941). Later work, including magnetic stratigraphy and biostratigraphic comparisons, suggests that the Gas Tank and Wagon Road faunas are Puercan and the Dragon fauna Torrejonian in age (Tomida and Butler 1980, Tomida 1981, Robison 1986). Archibald et al. (1987) tentatively assigned the Gas Tank to Pu2 (*Ectoconus / Taeniolabis taoensis* interval zone), Wagon Road to Pu3 (*Taeniolabis taoensis / Periptychus* interval-zone), and Dragon to To1 (*Periptychus / Tetraclaenodon* interval-zone). Both Pu2 and Pu3 are interpreted to occur within magnetic polarity chron 29N (Butler and Lindsay 1985); the Dragon fauna is considered to lie within anomaly 27N (Tomida and Butler 1980).

The Paleocene mammals of central Utah are of special interest in both temporal and geographic contexts: they fall within a time interval not well represented elsewhere, and they lie geographically between the classic sequence of the San Juan Basin, NM, and faunas from more northerly parts of the Western Interior (cf. Archibald et al. 1987: fig. 3.1). Mammals from the Paleocene of the North Horn Formation are not, in general, well known. We describe herein newly collected materials that provide further details on the morphology and systematics of some of the included taxa.

The approximate locations of the major mammal sites in the Paleocene part of the North Horn Formation, taken from data presented by Gazin (1941) and Robison (1986), are given in Figure 1. The materials described

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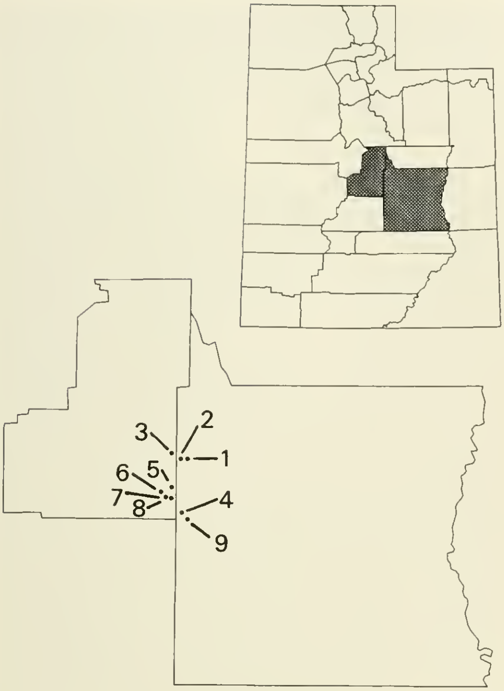

Fig. 1. Approximate locations of mammal-bearing sites in Paleocene part of North Horn Formation, Emery and Sanpete counties, UT; data from Gazin (1941) and Robison (1986). Localities, Dragon local fauna: Dragon Canyon (1). Wagon Road local fauna: Wagon Road (2), Wagon Road Ridge (3). Gas Tank local fauna: Gas Tank Hill (4), Dairy Creek (5), Jason Spring (6), Ferron Mountain (7; probably equivalent to OMNH V829), Blue Lake (8), and Sage Flat (9).

herein were collected in 1993–94, through surface prospecting methods. With one exception, all specimens are from the classic Dragon Canyon (Dragon local fauna; ?To1) and Wagon Road (Wagon Road local fauna; ?Pu3) sites described by Gazin (1941). The exception is a specimen assigned to *Ectoconus ditrigonus* (OMNH 28111), collected by Jon Judd of Castle Dale, UT, at a site south of Ferron Mountain. The site, OMNH V829, is probably the same as Robison's (1986) Ferron Mountain locality (Gas Tank local fauna; ?Pu2).

The following abbreviations are used for institutions cited in the text: BYU, Brigham Young University, Provo, UT; OMNH, Oklahoma Museum of Natural History, Norman; USNM, National Museum of Natural History, Washington, DC. Measurements, in mm, are as follows: L, anteroposterior length; W, transverse width; WTal, transverse width of talonid; WTri, transverse width of trigonid.

DESCRIPTIVE ACCOUNTS

Order Proteutheria

Family Pantolestidae Cope, 1884

?*Propalaeosinopa* sp.

Figs. 2A–B

MATERIAL.—OMNH 27681, fragment of right dentary bearing the talonid of P_4 (WTal = 1.5) and complete M_1 (L = 2.8, WTri = 1.8, WTal = 1.8).

LOCALITY AND HORIZON.—OMNH V800, "Wagon Road" locality (Gazin 1941, Robison 1986); Wagon Road local fauna, late Puercan (early Paleocene). Joes Valley Member, North Horn Formation, Emery County, UT.

DESCRIPTION AND DISCUSSION.—The dentary fragment includes the anterior root of P_4 and the anterior root of M_2. The anterior root of P_4 is bowed forward as in pentacodontids and most pantolestids, and its placement indicates that P_4 was relatively long, longer than M_1. The posterior mental foramen is large and is positioned between the posterior root of P_4 and the anterior root of M_1. The talonid of P_4 includes a large hypoconid and a small entoconid; these two cusps are united by a small, thin postcristid, forming a small talonid basin. The apex of the hypoconid is on the midline of the tooth, at the posterior termination of a cristid obliqua that angles lingually toward the front; the postcristid is oriented almost perpendicular to the cristid obliqua. Posterior to the postcristid and separated from it by a tiny transverse basin, a small cuspule (hypoconulid?) is present; this cuspule is connected to the hypoconid by a thin ridge. A tiny entoconulid, not connected to the other cusps, is present at the lingual base of the talonid basin.

The trigonid and talonid of M_1 are of equal width; the trigonid is distinctly higher than the talonid, though the tooth is moderately worn. The protoconid and metaconid are both triangular in occlusal outline and of equal occlusal area; the protoconid is the taller of the two cusps. The paraconid is small, low, and transversely oriented. Anterior and posterior carnassial notches are present in the paracristid and protocristid, respectively. Because of the transverse orientation of the paraconid, the paracristid forms an obtuse angle, with its apex at the anterior carnassial notch. A short anterior cingulum, which disappears at the anterolingual corner of the tooth, is present.

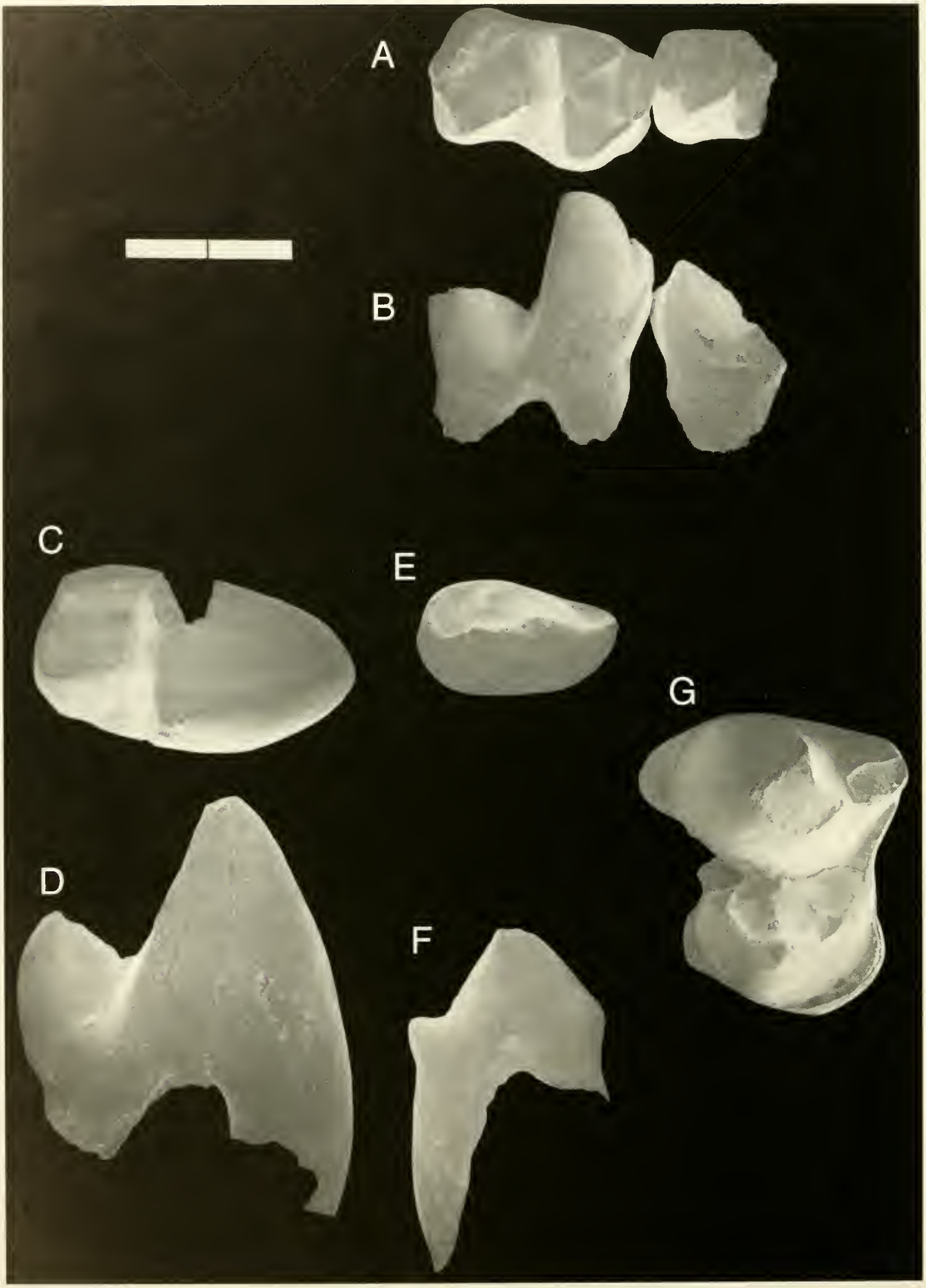

Fig. 2. Proteutheria from the North Horn Formation. A, B, P_4–M_1 of *Propalaeosinopa* sp. (OMNH 27681) in occlusal (A) and labial (B) views. C–G, *Aphronorus simpsoni* (OMNH 27667): C, D, right P_4 in occlusal and labial views, respectively; E, F, right P_3 in occlusal and labial views, respectively; G, left P^4 in occlusal view. Scale bar represents 2 mm; tooth roots and jaw fragments have been eliminated to improve clarity.

The posterior wall of the trigonid is planar; the cristid obliqua meets the base of the posterior wall of the trigonid below the posterior carnassial notch. Although it has been mostly obliterated by wear, an entoconulid (or at least an entocristid) appears to have been present anterior to the entoconid.

Of described species, OMNH 27681 most resembles the Torrejonian *Propalaeosinopa diluculi* (which we tentatively regard as distinct from *P. albertensis* following Rose 1981; see discussion in Van Valen 1967). However, the Utah taxon differs in several respects. The posterior mental foramen is more anteriorly located than in figured specimens of *P. diluculi* (Simpson 1936: fig. 3; Krause and Gingerich 1983: figs. 8, 9). M_1 of OMNH 27681 is long and narrow relative to the corresponding tooth of *P. diluculi*: it slightly exceeds published size ranges (Simpson 1937a, 1937b, Krause and Gingerich 1983) in length but not width. In the Utah taxon the cusps of M_1 are somewhat more robust and the postvallid wall more obliquely oriented with respect to the long axis of the tooth; the paracristid is higher, and the metaconid lower, than in *P. diluculi*. The talonid of P_4 is broader and more basined than in *P. diluculi* (or other species of the genus). We regard the specimen from the North Horn Formation as representing a distinct species, but materials in hand are inadequate to properly diagnose and circumscribe it. Gazin (1941) briefly described two morphs, represented by upper molars, as generically undetermined pantolestids; both were from the Dragon local fauna. Of these, he found pantolestid "a" to compare favorably with *Bessoecetor* (=*Propalaeosinopa*), differing from "*B. thomsoni*" (=*P. diluculi*) in being slightly larger and in a few morphological details. It is possible that pantolestid "a" and OMNH 27681 represent the same species, although we point out that they derive from different horizons in the North Horn Formation. Differential representation precludes direct comparison with OMNH 27681.

If referral of the newly recovered specimen to *Propalaeosinopa* is correct, it represents the oldest record of the genus and of the family Pantolestidae, a somewhat aberrant group of enigmatic affinities. The new occurrence is estimated to be late Puercan (Pu3) in age; the genus and family are otherwise first known from the late Torrejonian (To3; Archibald et al. 1987). In this context, we note that several morphological details show the North Horn taxon to be distinct, at the species level at least, from described species; when better known, it may prove to be generically separable.

Family Pentacodontidae
(Simpson, 1937) Van Valen, 1967
Aphronorus simpsoni Gazin, 1938

Figs. 2C–G

NEWLY REFERRED MATERIAL.—OMNH 27667, right dentary fragment with P_{3-4} ($P_3L = 2.4$, $W = 1.4$; $P_4L = 4.0$, $W = 2.5$) and associated left P^4 ($L = 3.3$, $W = 4.1$).

LOCALITY AND HORIZON.—OMNH V799, "Dragon" locality (locality 2 of Gazin 1941: p. 7, fig. 1), Dragon local fauna, early Torrejonian (early or middle Paleocene). Joes Valley Member, North Horn Formation, Emery County, UT.

DESCRIPTION AND DISCUSSION.—OMNH 27667 differs from the type of *A. simpsoni* (USNM 15539) in minor ways but is clearly referable to the species. P_4 is slightly larger than in the type and differs in having a weaker anterior cingulum, which is barely indicated on the anterolingual part of the tooth and is completely absent labial to the keel extending down the anterior face of the protoconid. The minute ridge that extends down the posterior wall of the metaconid (to meet with the cristid obliqua) is lacking; however, the development of this ridge in the type may be due partly to the advanced wear in that specimen. P_4 of OMNH 27667 bears a small but distinct entoconid; this region of the tooth is broken in USNM 15539. The anterior end of P_4 in OMNH 27667 is slightly more developed downward than in USNM 15539, vaguely recalling the more advanced condition seen in *Pentacodon* (Simpson 1937a: 124). Unlike either species of *Pentacodon*, however, the P_4 lacks a basal paraconid, the protoconid is not as inclined posteriorly from base to apex, and the talonid is better developed.

P_3 has not been previously figured or described for *Aphronorus simpsoni*, though this tooth is known for *A. fraudator* (illustrated in outline by Simpson 1937a, Gazin 1941). P_3 of OMNH 27667 is more anteroposteriorly elongate than in *A. fraudator*. The tooth is distinctly two-rooted and is much smaller than P_4; maximum width occurs just posterior to the protoconid. A small talonid basin is developed, with a minute hypoconid and a "cristid obliqua" connected to a ridge running down the posterior flank of the protoconid. A small, short ridge and swelling on the posterolingual flank of the protoconid are suggestive of a metaconid. A faint cingulum is present anterolingually.

No associated upper teeth have been previously described for *Aphronorus simpsoni*, although a few isolated specimens may belong to the species (Gazin 1941, Robison 1986). P^4 of OMNH 27667 is broken near the paraconule and at the lingual edge of the tooth, between the cingulum at the base of the protocone and the lingual root; the labial side of the metaconid is also damaged. Three roots are present. The tooth, although similar to P^4 of *A. fraudator*, differs in several respects. The parastyle is absent; a small paraconule is present; a metaconule as such is lacking, although there is a vague swelling of enamel in this position. The basal protoconal cingula show no tendency to develop cuspules, as they do in *A. fraudator*, and the metacone is much smaller in size, relative to the paracone, than in that species. The labial cingulum of P^4 in OMNH 27667 is also less developed than in *A. fraudator*.

Aphronorus simpsoni was diagnosed as distinct from the comparatively well-known *A. fraudator* mainly on the basis of differences in proportions of P_4 and the lower molars (Gazin 1941). OMNH 27667, which includes teeth previously unreported for *A. simpsoni*, shows that it is further distinct in having a somewhat more elongate P_3; P_4 has a narrower, smaller-basined talonid. P^4 differs from that of *A. fraudator* in several respects, including the lack of a metaconule and parastyle, and the much lesser development of the metacone. Considering the specializations of the posterior premolars in pentacodontids (Simpson 1937a) and the possibility that they represent a relatively archaic group (Van Valen 1967), it is difficult to judge which conditions are apomorphous, although some of the states possessed by *A. simpsoni* (e.g., smaller P_4 talonid; P^4 with small metacone and no metaconule) would appear—by comparison to more primitive Eutheria—to be primitive. The Tiffanian species *A. orieli*, known by remarkably complete specimens (Gingerich et al. 1983), appears to be considerably more advanced, with greatly expanded crushing surfaces (particularly the protocone) on P^4.

Order Condylarthra
Family ?Arctocyonidae
(Giebel, 1855) Murray, 1866
Desmatoclaenus hermaeus Gazin, 1941

Fig. 3A

NEWLY REFERRED MATERIAL.—OMNH 27682, associated skull and jaw fragments with broken right and left P^4 (right $P^4L = 6.5$), right M^{1-3} ($M^1L = 7.3$, $W = 8.6$; $M^2L = 7.3$, $W = 11.0$; $M^3L = 6.2$, $W = 8.7$), left M^{2-3} (M^2 broken, $L = 7.4$; $M^3L = 6.0$, $W = 8.8$), left M_1 ($L = 8.8$, $WTri = 7.2$, $WTal = 7.4$), talonid of right M_2 ($W = 6.4$), trigonid of left M_2 ($W = 6.0$), and talonid of right M_3 ($W = 5.2$).

LOCALITY AND HORIZON.—OMNH V800, "Wagon Road" locality (Gazin 1941, Robison 1986); Wagon Road local fauna, late Puercan (early Paleocene). Joes Valley Member, North Horn Formation, Emery County, UT.

DESCRIPTION AND DISCUSSION.—P^4 has distinct conules, with the paraconule being taller than the metaconule. These cusps have not previously been noted for P^4 of the species, perhaps because of wear on the type specimen (USNM 16202; see Gazin 1941: fig. 19; West 1976: fig. 2). The upper molars have a labial cingulum that is continuous. Interruption of the ectocingulum at the base of the paracone was cited as a generic character of *Desmatoclaenus*. However, the cingulum is complete in other specimens, such as BYU 3800 (Robison 1986: pl. 2, fig. 10), and we regard this as a feature that is intraspecifically variable. M^3 bears a small but distinct cingular hypocone, another character that is apparently variable in the species (Gazin 1941: figs. 19, 20; Robison 1986). The only variation worthy of note in the lower dentition of OMNH 27682 is the hypoconulid of M_3, which apparently projected posteriorly as a distinct lobe, unlike the condition seen in USNM 16202 (Gazin 1941: fig. 19).

Gazin (1941) originally described two species of *Desmatoclaenus*, *D. hermaeus* and *D. paracreodus*, both from the Wagon Road fauna. West (1976) synonymized the two, a view apparently shared by Tomida and Butler (1980), but Robison (1986) recognized them as distinct and reported additional materials of both species from other localities. In the original diagnosis (Gazin 1941), *D. paracreodus* was said to be larger than *D. hermaeus*, with the lingual portion of upper molars more inflated and with a relatively larger M^3, bearing a better-

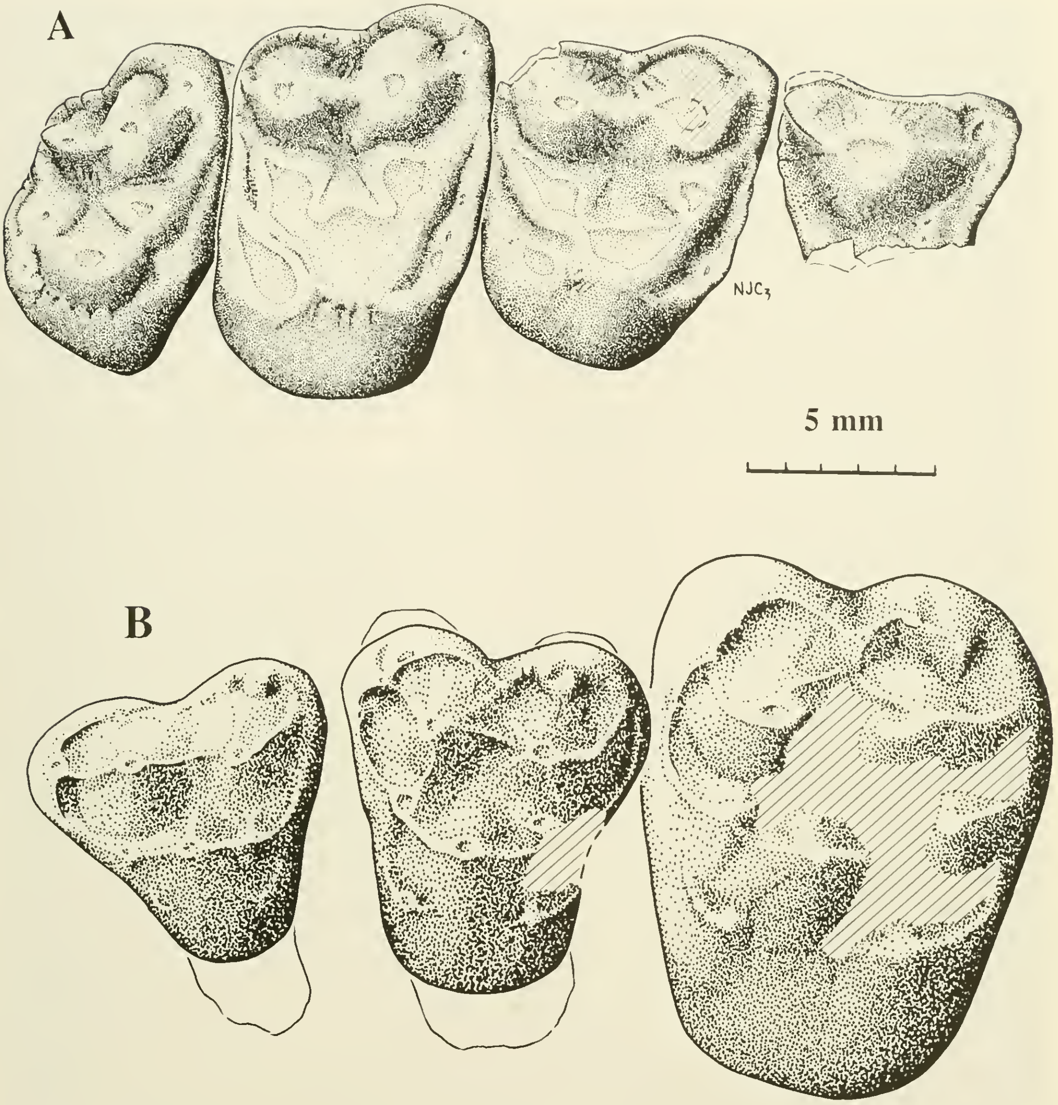

Fig. 3. ?Arctocyonidae and Periptychinae from the North Horn Formation. A, right P^4–M^3 of *Desmatoclaenus hermaeus* (OMNH 27682) from the North Horn Formation; base of M^2 restored from contralateral tooth of same specimen, and maxilla eliminated to improve clarity; B, left dP^{3-4} and M^1 of *Ectoconus ditrigonus* (OMNH 28111) in occlusal view; maxilla eliminated to improve clarity.

developed hypocone. As shown by West (1976), these differences in size and morphology are both minor and inconsistent. In this context, we note that M^{1-2} of OMNH 27682 are relatively small (a supposed character of *D. hermaeus*), yet M^3 is proportionately large, with a well-developed hypocone (characters cited for *D. paracreodus*). We follow West (1976) in regarding the species as synonymous.

In the original diagnosis and discussion of *Desmatoclaenus*, Gazin (1941) compared the genus with *Tetraclaenodon* and *Protogonodon*, as the latter taxon was then conceived (Matthew 1937, Simpson 1937a). Van Valen (1978) placed "?*P.*" *protogonioides* (cf. Matthew 1937)—originally referred (Cope 1882a), in part, to the genus *Mioclaenus*—in *Desmatoclaenus*, adding to the genus two additional species, *D. dianae* and *D. mearae*; *Protogonodon* was synonymized with *Loxolophus*. We are in agreement with these assignments; *D. protogonioides* is relatively well represented and adds significantly to knowledge of the genus. Thus recognized, *Desmatoclaenus* is distinct from *Loxolophus* in having stronger protocones on P^{3-4}; better-developed, more lingually placed hypocone on M^{1-2}, with hypocone occasionally distinct on M^3; and paraconid of lower molars placed more posterolingually and closely appressed to the metaconid. *Desmatoclaenus* differs from *Tetraclaenodon* in having less molarized premolars (a metacone is lacking on P^{3-4}; the trigonid is poorly developed and a talonid basin is lacking on P_4), upper molars lacking mesostyle and with lesser development of the hypocone; and lower molars with more distinct, anteriorly placed paraconid.

Gazin (1941) considered *Desmatoclaenus* to be structurally intermediate between the archaic ungulate "*Protogonodon*" (then considered a creodont) and *Tetraclaenodon*, a primitive phenacodontid; the differential comparisons presented above uphold this view. Subsequent workers have referred *Desmatoclaenus* to the Arctocyonidae on the one hand (Van Valen 1978, Cifelli 1983) or the Phenacodontidae on the other (Simpson 1945, West 1976, Robison 1986). The positioning of the upper molar hypocone somewhat more lingually in *Desmatoclaenus* than in *Loxolophus* is vaguely reminiscent of the presumably derived condition in the Phenacodontidae; similarly, the low, bunodont cusps bearing mainly flat, apical wear are similar to conditions generally obtained in members of that family. *Desmatoclaenus* may well be a transitional taxon, but in the absence of compelling evidence in the form of synapomorphies, we here tentatively retain it in the Arctocyonidae. In this context, we note that the referred species *D. protogonioides* apparently has a reduced anterior dentition, a condition shared with loxolophine arctocyonids (Cifelli 1983).

Family Periptychidae Cope, 1882

Anisonchus ?oligistus Gazin, 1941

Fig. 4A

NEWLY REFERRED MATERIAL.—OMNH 27679, right M^3.

LOCALITY AND HORIZON.—OMNH V800, "Wagon Road" locality (Gazin 1941, Robison 1986); Wagon Road local fauna, late Puercan (early Paleocene). Joes Valley Member, North Horn Formation, Emery County, UT.

DESCRIPTION.—OMNH 27679 is missing the lingual base of the crown and enamel from the posterior margin of the tooth; its estimated L is 3.1. This specimen is appropriate in size for only two of the four species of *Anisonchus* reported from the North Horn Formation (Gazin 1941, Robison 1986); OMNH 27679 differs from M^3 referred to *A. athelae* (including *A. eowynae*; Robison 1986) and is tentatively referred to *A. oligistus*, for which M^3 was not previously known. Although the tooth is incomplete and worn, it can be seen that the anterocingulum was relatively weak and lacked a pericone. Similarly, the hypocone was weak in comparison to the condition in *A. athelae*, being more similar to the larger *A. dracus* in this respect. The pattern of wear suggests that both paraconule and metaconule were present, placed near the base of paracone and metacone, respectively.

Haploconus elachistus Gazin, 1941

Figs. 4B–F

NEWLY REFERRED MATERIAL.—OMNH 27670, fragments of mandible with left M_{1-2} (M_1L = 3.8, WTri = 2.7, WTal = 2.8; M_2L = 3.9, WTri = 3.2, WTal = 2.9) and right M_2 (L = 4.0, WTri = 3.1, WTal = 3.0); 27713, fragments of left mandible with P_3 (L = 4.5, W = 2.8) and a heavily encrusted molar; OMNH 27680, right P_4 (L = 4.5, W = 3.3).

LOCALITY AND HORIZON.—OMNH V800, "Wagon Road" locality (Gazin 1941, Robison 1986); Wagon Road local fauna, late Puercan (early Paleocene). Joes Valley Member, North Horn Formation, Emery County, UT.

DESCRIPTION AND DISCUSSION.—Available lower premolars (OMNH 27680, 27713) are too worn to determine whether a paraconid was present; Gazin (1941) reported the presence of this cusp on P_3 but not P_4 of *Haploconus elachistus*. The protoconid is a large, inflated cusp, particularly on P_4. A talonid crescent extends posteriorly from the lingual base of the protoconid, curving labially at the posterior margin of both P_3 and P_4. The metaconid of lower molars is nearly as tall as the protoconid and is transversely aligned with that cusp; a weak paracristid descends anterolingually from the protoconid, terminating in a small paraconid, which lies in a median position. As described by Gazin (1941), the pre-entocristid is taller than the cristid obliqua. The entoconid forms a distinct pillar and projects somewhat on the

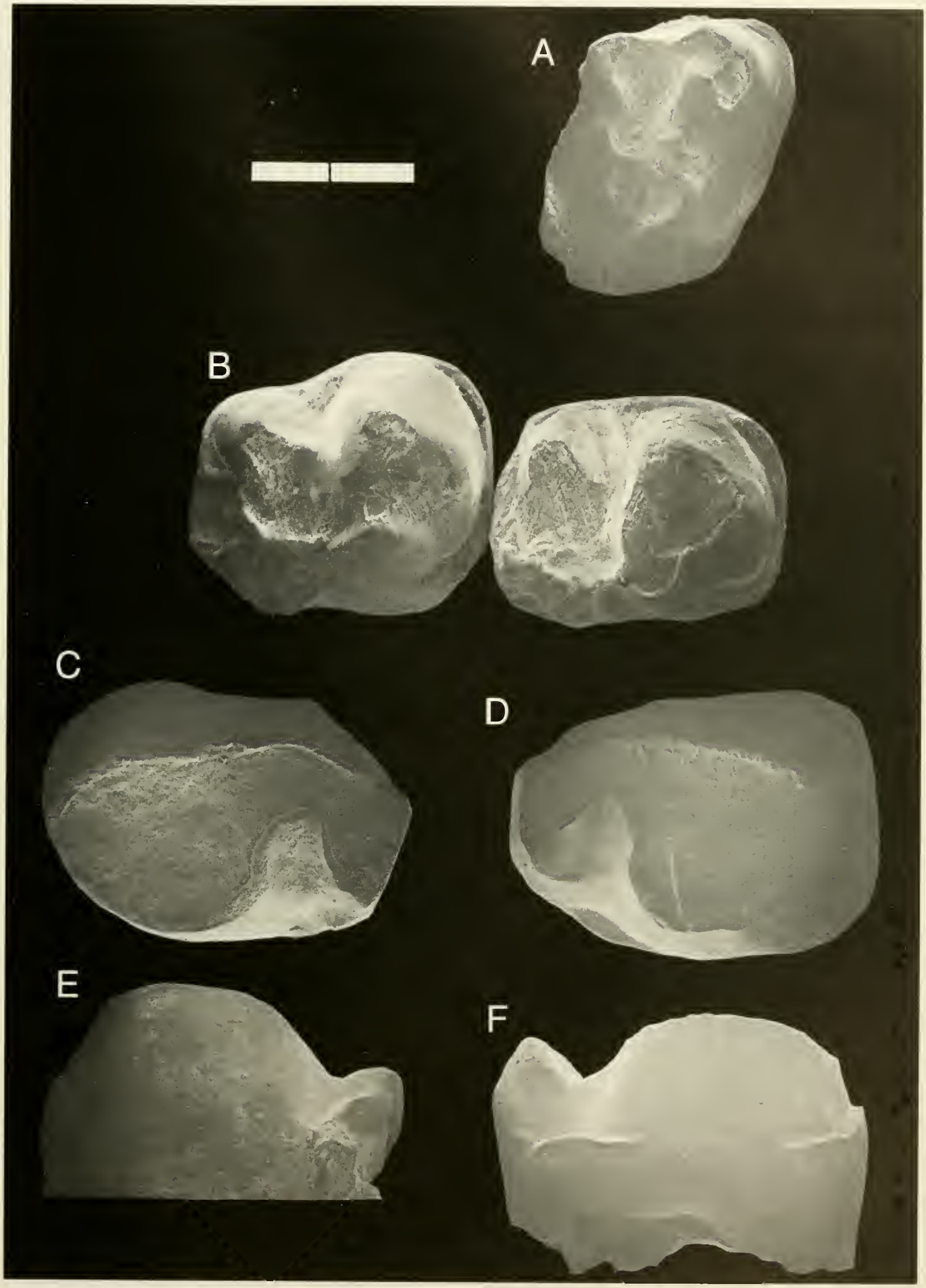

Fig. 4. Anisonchinae from the North Horn Formation. A, *Anisonchus ?oligistus* (OMNH 27679, right M^3 in occlusal view). B–F, *Haploconus elachistus*: B, left M_{1-2} (OMNH 27670) in occlusal view; C, E, left P_3 (OMNH 27713) in occlusal and labial views, respectively; D, F, right P_4 (OMNH 27680) in occlusal and labial views, respectively. Scale bar represents 2 mm; tooth roots and jaw fragments have been eliminated to improve clarity.

lingual side of the tooth; the hypoconulid forms a fingerlike projection at the back of the tooth and is somewhat lingual in position, an appearance emphasized in later wear stages.

Two species of *Haploconus*, *H. angustus* and the larger *H. corniculatus*, are recognized from the Torrejonian (To2; Archibald et al. 1987) of the San Juan Basin, NM (Matthew 1937). The apparent last record of *Haploconus* is represented by a single molar, of uncertain specific affinities, from Swain Quarry (To3?; Archibald et al. 1987), WY (Rigby 1980). The genus is otherwise known only from the North Horn Formation. Gazin (1939) described *H. inopinatus* from the Dragon fauna, later adding a second species, ?*H. elachistus*, from the Wagon Road (Gazin 1941). More recently, Robison (1986) has reported specimens of *Haploconus* sp. from the Gas Tank local fauna; these materials are of interest in documenting the first appearance of the genus, but unfortunately they are not specifically diagnostic. *H. inopinatus*, of To1 age, is similar in size to the later *H. angustus* but differs from that species in proportions of the upper molars (Gazin 1939). *H. elachistus*, the geologically oldest described species, is smaller than the Torrejonian species and, as noted by Gazin (1941), differs from them in a number of respects. In the lower dentition, P_{3-4} are less inflated than in *H. angustus*. Similarly, the trigonids of lower molars in *H. elachistus* lack the inflated appearance seen in Torrejonian species; a small paraconid is still present, whereas in remaining species the paracristid forms a bladelike surface extending anteriorly from the protoconid and bears no cusp. Lower molars of *H. elachistus* also lack the crenulated or striated enamel and prominent labial cingulum seen in other species. As might be expected, the geologically older *H. elachistus* appears to be more primitive than the Torrejonian species for the characters cited. In this context the apparent presence of a more derived species in the Gas Tank local fauna (Robison 1986) is somewhat surprising.

Haploconus is distinctive in the extreme modification of lower molar trigonids (with reduction to loss of the paraconid) and in the unusual configuration of the talonid in posterior lower premolars (with a lingual rather than labial crescent), characters that are both expressed in *H. elachistus*. The affinities of the genus are puzzling; Gazin (1941), noting the primitiveness of some features of *H. elachistus*, considered the species to be transitional between *Conacodon* and more derived species of *Haploconus*. In retaining unreduced lower molar trigonids and relatively unspecialized lower premolars, species of *Conacodon* are primitive with respect to *Haploconus*. In terms of characters that are probably derived within the context of Condylarthra, *Conacodon*, *Haploconus*, and *Oxyacodon* have a lingually placed hypoconulid and hypertrophied postmetacristid on lower molars, lingually placed hypocone on upper molars, loss of protocone on P^3, and, possibly, a columnar, lingually placed entoconid on lower molars (not clearly seen in all species of *Oxyacodon*). However, the exclusiveness of these characters and their potential status as synapomorphies remain to be established. Archibald, Schoch, and Rigby (1983) have shown that *Conacodon* and *Oxyacodon* represent a distinctive subfamily, Conacodontinae, whose relationship to other periptychids is unclear; further investigation of the position of *Haploconus* with respect to this clade is clearly warranted.

Ectoconus ditrigonus (Cope, 1882)

Fig. 3B

NEWLY REFERRED MATERIAL.—OMNH 28111, fragment of left maxilla with dP^{3-4} and M^1 ($dP^3L = 7.5$, $W = 7.0$; $dP^4L = 7.5$, $W = 8.4$; $M^1L = 9.6$, $W = 13.5$).

LOCALITY AND HORIZON.—OMNH V829, probably the same as Robison's (1986) Ferron Mountain locality; Gas Tank local fauna, middle Puercan (early Paleocene). Joes Valley Member, North Horn Formation, Emery County, UT.

DESCRIPTION AND DISCUSSION.—The deciduous teeth, dP^{3-4}, are markedly smaller than M^1; both have conspicuous parastylar and metastylar lobes. The third deciduous premolar has a roughly triangular occlusal profile and is longer than it is wide. The paracone and metacone are subequal in height; a large parastyle is present almost directly anterior to the paracone. A prominent ridge extends lingually from the parastyle to the protocone, which is nearly as tall as the paracone and metacone; another ridge descends the labial slope of the parastyle, continuing posteriorly as a weak ectocingulum. Labial to the metacone, the stylar shelf broadens; a small cusp, serially analogous (if not homologous) to a similar cusp on upper molars of *Ectoconus ditrigonus* (Osborn and Earle 1895), is present labial to the metacone. A salient postmetacrista descends posterolabially from the apex of the metacone, extending to the posterolabial corner of the tooth. Weak paraconule and metaconule are present on the pre- and postprotocrista, respectively. Faint pre- and postcingulae are present on the lingual slopes of the protocone. The fourth deciduous premolar is more molariform than dP^3, differing from M^1 in having smaller conules and associated cristae, and in the lesser development of the protocone region. The parastyle of dP^4 is more labially placed than on dP^3, and the ectocingulum and cingular cusp better developed than on that tooth; a small mesostyle is also present. The lingual cingulae are strong; pericone and hypocone are present. M^1 is typical of *Ectoconus* and complete description is unnecessary. The ectocingulum is strong and bears both a mesostyle and posterior stylar cusp. The latter is subconical and is connected to the base of the metacone by a low ridge. Paracone, metacone, and protocone are subequal in height; conules are strongly developed and are only slightly lower than the principal cusps.

Ectoconus ditrigonus, the type species, was first described on the basis of material from the San Juan Basin, NM (Cope 1882b). Matthew (1937) reported a second species from the San Juan Basin, *E. majusculus*, considered by Van Valen (1978) to be synonymous with *E. ditrigonus*. The genus is known from several localities, including both Pu2 and Pu3 horizons, in that area (Archibald et al. 1987). Gazin (1941) described the species *E. symbolus* from the Wagon Road (?Pu3) fauna, North Horn Formation. Robison (1986) described additional materials of *E. symbolus* from localities of the Gas Tank fauna, thereby extending the range of the species to ?Pu2, and reported *E. ditrigonus* from two Gas Tank localities. OMNH 28111 can be referred to the latter species on the basis of size (larger than *E. symbolus*) and the presence of a relatively small posterior cusp, connected to the base of the metacone by a low ridge, on the ectocingulum of M^1 (Robison 1986).

Deciduous teeth of archaic ungulates have not been widely described or illustrated, a notable exception being the deciduous premolars of Phenacodontidae (West 1971). To our knowledge, deciduous teeth of Periptychidae have not been previously described, so that there is no basis for comparison with dP$^{3-4}$ of *Ectoconus ditrigonus*.

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SPRINGTIME MOVEMENTS, ROOST USE, AND FORAGING ACTIVITY OF TOWNSEND'S BIG-EARED BAT (*PLECOTUS TOWNSENDII*) IN CENTRAL OREGON

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ABSTRACT.—Seasonal movements, roost-site fidelity, and foraging activity patterns are largely unknown for western populations of Townsend's big-eared bat (*Plecotus townsendii*). We used miniature radiotelemetry units to track springtime movements of six bats inhabiting forested lava flows in central Oregon, and found that bats moved up to 24 km from hibernacula to foraging areas. Individual bats returned to the same foraging area on successive nights but shifted to different areas in presumed response to changes in insect availability. Both sexes apparently use a series of interim roost sites between emergence from hibernation and the time females enter into maternity colonies, with little individual fidelity to these sites. In regions characterized by extensive lava-flow topography, suitable daytime roosts are numerous and dispersed over a large area, allowing bats to move relatively great distances to locate foraging ranges. Hence, the actual area of concern for effective management of individual populations can be considerably larger than indicated solely by locations of hibernacula and maternity caves of this declining species.

Key words: Townsend's big-eared bat, Plecotus townsendii, *foraging movements, roost sites, roost fidelity, hibernacula, caves, central Oregon, radiotelemetry, lava flows, candidate species.*

Townsend's big-eared bat (*Plecotus townsendii*) is distributed over much of western North America (Hall 1981), although populations may be widely scattered within its range. The species appears to be a habitat generalist, reportedly inhabiting coniferous forests in northern New Mexico (Jones 1965), mixed mesophytic forests in Kentucky (Adam et al. 1994), deserts in Arizona (Hoffmeister 1970), native prairie in Kansas and Oklahoma (Humphrey and Kunz 1976), riparian communities in northeastern Montana (Swenson and Shanks 1979), Kansas, and Oklahoma (Humphrey and Kunz 1976), and agricultural areas and coastal regions in California and Washington (Dahlquest 1947, 1948, Pearson et al. 1952). In Oregon the distribution of Townsend's big-eared bat is discontinuous and highly local across forest and shrubsteppe habitats throughout the state (Perkins and Levesque 1987).

Two disjunct subspecies occur in eastern North America, both of which are listed as endangered under the U.S. Endangered Species Act. Kunz and Martin (1982) suggested that western populations also are vulnerable, especially to disturbance in winter hibernacula and summer maternity caves. Both subspecies found in the western United States are declining markedly (Perkins and Levesque 1987, Pierson et al. 1991), and the species is listed as endangered, sensitive, or of special concern by several western states and federal land management agencies.

Big-eared bats feed almost exclusively on Lepidoptera (Ross 1967, Whitaker et al. 1977, 1981, Dalton et al. 1986, Sample and Whitmore 1993) and are viewed as moth specialists (Dalton et al. 1986, Sample and Whitmore 1993). Probably most limiting to their distribution, however, is availability of suitable sites for roosting, hibernation, and reproduction, which consist primarily of caves and abandoned mines. These three activities require different microclimatic conditions (Dahlquest 1947, Pearson et al. 1952, Twente 1955, Barbour and Davis 1969, Martin and Hawks 1972, Humphrey and Kunz 1976, Marcot 1984, Genter 1986, Perkins and Levesque 1987, Pierson 1989, Pierson et al. 1991, Lacki et al. 1993, Clark et al. 1995). Any single site generally is unsuitable for more than one function, although microclimates in different regions of the same cave sometimes differ sufficiently to accommodate more than one activity (e.g., Clark et al. 1995).

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Big-eared bats are colonial for most of the year, but colony dynamics and seasonal movements have not been studied in the Intermountain West. In central Oregon, *P. townsendii* undergoes arousal from hibernation and movement from hibernacula in April, although the precise timing of these events appears to vary with weather conditions and topography (U.S. Forest Service, Deschutes National Forest, unpublished data). Females form maternity colonies in late spring or early summer (USFS unpublished data), but the timing of their arrival at maternity roosts is poorly documented, and it is unclear whether they move immediately to maternity roosts upon departure from hibernacula.

A much better understanding of seasonal movements among roost sites is necessary for effective management of populations. Although it is clear that traditional site use (sensu Dobkin et al. 1986) occurs for specific hibernacula and maternity roosts, the extent of roost site fidelity by individual bats is unknown. Recent telemetry studies have been conducted for both endangered subspecies found in eastern North America (Clark et al. 1993, Adam et al. 1994, Lacki et al. 1994), but no telemetry studies have examined the movements of western subspecies. Our primary objective was to acquire information concerning the extent of movements by individual Townsend's big-eared bats during the period following arousal from hibernation in an area containing a significant proportion of Oregon's known population.

STUDY AREA AND METHODS

Fieldwork was conducted in Deschutes County on the Fort Rock Ranger District of the Deschutes National Forest and adjacent lands administered by the Bureau of Land Management. The primary study area (Fig. 1) consists of a NW-SE–oriented basin containing extensive forested lava flows, and the surrounding buttes from 44°25′ to 43°37′ N, and 121°15′ to 120°48′ W. Elevations range from 1400 m on the basin floor to nearly 2000 m atop Pine Mountain. Forests are open stands of ponderosa pine (*Pinus ponderosa*) with bitterbrush (*Purshia tridentata*), manzanita (*Arctostaphylos* spp.), and bunchgrass understories. Scattered, relatively closed, stands of lodgepole pine (*P. contorta*) also occur throughout. Areas adjacent to lava flows consist of shrub-steppe habitat dominated by sagebrush (*Artemisia tridentata*).

The study area lies within the broad zone of intergradation between the western interior form (*P. t. pallescens*) and the coastal Pacific form (*P. t. townsendii*) of Townsend's big-eared bat (Handley 1959). We concur with Handley's (1959: 199) assessment that "allocation . . . from much of this area to one race or the other is largely a matter of personal opinion."

Based on USFS cave surveys conducted from 1985 to 1991, two hibernacula (S1 and S2, Fig. 1) but no maternity caves were known from the southern end of the basin. The northern end of the basin contained a series of hibernacula and one maternity cave (N3, which was gated), as well as one other cave (N2) that reportedly was used as a maternity roost in the past. The maternity cave and the northernmost hibernaculum in the southern portion of the basin are separated by 30 km, which prompted the assumption that big-eared bats in the basin consisted of two separate populations (J. M. Perkins, unpublished report to USFS). Subsequent to completion of our fieldwork, a previously unknown maternity cave was discovered beyond the southern end of the basin, 17 km southeast of S1.

Fieldwork in 1992 commenced on 7 April and continued through 9 June. Six big-eared bats (5 females, 1 male) were captured by hand between 1100 and 1730 h from four different caves in April and May (Table 1). Each bat was fitted with a battery-powered (14–21 day battery longevity), miniature radiotransmitter (0.6–0.7 g; Model BD-2B, Holohil Systems, Ltd.) affixed to the dorsal, interscapular fur (Dobkin et al. in press) with eyelash cement. Transmitter units averaged 6% of bat body mass ($\bar{x}$ = 10.6 g, Table 1), which should have had minimal effect on maneuverability and energy costs for this species (Davis and Cockrum 1964, Aldridge and Brigham 1988).

Bats carrying transmitters were tracked with portable receivers (Telonics) equipped with directional antennae (Wilkinson and Bradbury 1988). Bats were monitored for nearly 850 observer hours over the 64-day period through a combination of daytime ground searches and nighttime triangulations from fixed locations. Two or three observers with receivers were located on the tops of buttes widely separated around the basin (Fig. 1) to provide the directional data necessary for

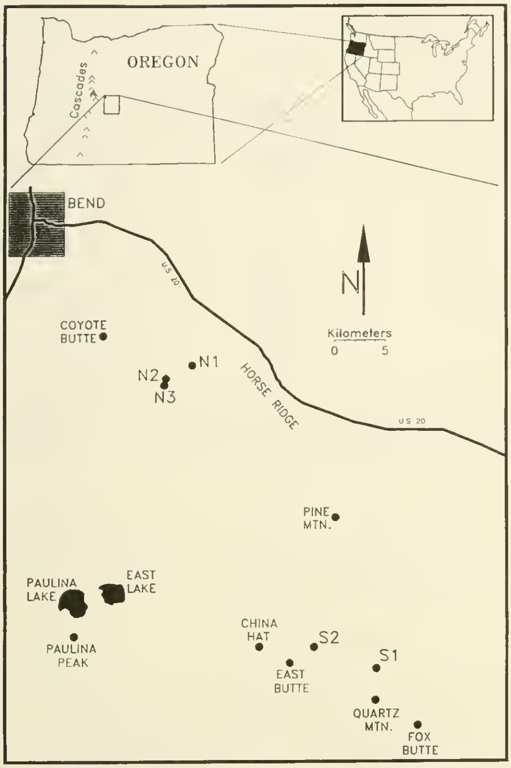

Fig. 1. Map of the study area in central Oregon showing locations of the four caves in which Townsend's big-eared bats were captured and fitted with radiotransmitters (S1, S2, N1, and N2), and location of the only known maternity cave (N3) in the basin. Telemetered bats were monitored from atop Pine and Quartz mountains, Coyote, East, Fox, and China Hat buttes.

determining bat locations. The monitoring protocol for fixed-point triangulation consisted of scanning all active frequencies for the initial five minutes of each quarter hour. If contact was made, the other observers were notified by radio and the bat was tracked continuously. In addition, seven flights were made at night by fixed-wing aircraft carrying a receiver and wing-mounted antennae and equipped with a LORAN system. LORAN fixes were integrated with simultaneous directional information obtained from ground-based receivers.

We conducted ground searches on foot and from moving vehicles. Efforts were concentrated in the vicinity of caves known to be used by bats, including caves in which telemetered bats originally were captured. These searches continued for 7–14 days following attachment of transmitters. Due to rugged topography and the distances between northern and southern ends of the basin, only southern caves were checked systematically following tagging of the first three bats, all of which were from the southern basin. Likewise, only northern caves were checked systematically following tagging of the last three bats, all of which came from the northern basin. All caves were checked as opportunity permitted, resulting in essentially complete coverage of all known cave sites in the basin at least weekly.

Results

Movements and Roost Site Fidelity

All marked females left their caves within two nights of capture and neither returned to these caves nor entered the known maternity cave (N3) during the remainder of transmitter battery life. Upon emergence from their hibernacula, all three females from the southern end of the basin moved 11–12.5 km northeast to the western slopes of Pine Mountain and did not return to the vicinity of their hibernacula in the southern end of the basin. Only female #579 was located subsequently, again on the western slope of Pine Mountain. Faint signals were received briefly from one of these females on 3 May on a precise bearing toward the then-unknown maternity cave southeast of the study area.

The most extensive telemetry data were collected for female #707, which left N1 on the second night following capture. She was located again five nights later and was tracked for the following five nights (including a series of LORAN fixes made from the air), and then to a day roost located just east of the crest of Pine Mountain, ca 20 km from N1 but only 2–4 km from where she had been foraging on the preceding five nights. Although we do not know whether she had used this roost previously, she was not found there subsequently. This bat went undetected over the next three nights and was then located for the last time on the following night. All foraging locations beyond the immediate vicinity of N1 were on the western slope of Pine Mountain, 17–24 km from N1.

Foraging locations for the fifth female (#728) were within 2–5 km of N2: southwest of N2 on one night and northeast of N2 two nights later. This bat dropped her transmitter, which we recovered 15 days after attachment, at a location 5 km west of N2 and within 1 km

TABLE 1. Summary of radiotelemetry contacts with Townsend's big-eared bats carrying transmitter units on the Deschutes National Forest in central Oregon, 1992.

Bat #	Location[a]	Max. distance[b] (km)	Sex	Mass (g)	Dates of contact
558	S1	11	F	11.0	17–19 April
568	S2	11	F	11.2	17–19 April
579	S1	12	F	12.0	19 April–2 May
707	N1	24	F	10.3	28 April–10 May
728	N2	5	F	10.6	12–25 May[c]
768	N2	8	M	9.0	20–26 May

[a] Indicates location of cave where bat was captured and fitted with radiotransmitter. To maintain site security, caves are designated by alphanumeric codes; S and N indicate cave location in southern and northern portions of the study area, respectively. S1, S2, and N1 were winter hibernacula; N2 was an interim roost site.
[b] Maximum distance moved from cave of initial capture, as determined by radio contact with foraging bat.
[c] Transmitter dropped from bat on 26 or 27 May and recovered on 27 May.

of unnamed caves known to have harbored big-eared bats occasionally in the past (L. Becker, unpublished USFS survey data).

The single telemetered male (#768) foraged extensively in the immediate vicinity of N2 upon evening emergence, then moved 6–8 km east to forage over Horse Ridge. This bat was not located again until five nights later, when he returned to N2, and was recorded over the next two nights foraging in and around the sinkhole immediately in front of N2. Although male #768 returned to roost for two consecutive days in the cave where originally captured, he then left and did not return again prior to the end of fieldwork 12 days later.

The habitat used for foraging consisted of sagebrush shrubsteppe (western slopes of Pine Mountain and Horse Ridge) and very open ponderosa pine woodland with extensive bitterbrush and interspersed areas (<5 ha) of sagebrush. Relatively little time appeared to be spent foraging in more densely forested areas.

Times of Activity

Big-eared bats emerged from their cave roosts to forage shortly after sunset, with time of emergence becoming later as day length increased in the spring (Fig. 2). Although our data are very limited, an interpretable pattern of activity can be seen in the May data. Big-eared bats foraged in the immediate vicinity of their cave roosts during the first few hours of darkness, moved to areas farther from their roost to forage (perhaps intermittently) from around midnight to within an hour or two of sunrise, and then once again returned to forage in the vicinity of their day roost.

DISCUSSION

Continuous monitoring of movements and activity in small, cave-dwelling bats like Townsend's big-eared bat is constrained by (1) the need to minimize load mass carried by an animal, which strongly limits both strength of transmitter signal output and battery longevity, and (2) the difficulty of signal detection in landscapes of rugged, rocky topography and from within caves. Despite these limitations, a number of salient points can be deduced from our study.

Our data clearly indicated that female big-eared bats in central Oregon did not move directly from their winter hibernacula to maternity caves, but instead utilized a series of interim roost sites over a period of perhaps as much as two months. The four females marked in April were captured in winter hibernacula in the company of other roosting conspecifics. In contrast, the two bats captured in May were the only big-eared bats roosting in the cave on the dates of capture; we assumed that neither of these bats hibernated in N2 during the preceding winter, although we cannot exclude this possibility. None of the four caves in which bats were captured was used as a maternity cave.

We suggest that little fidelity to interim roost sites occurs because neither of the two females found in day roosts returned to these roosts on subsequent days. In addition, male #768 left his roost cave, returned five days later, remained for two days, and then left again for at

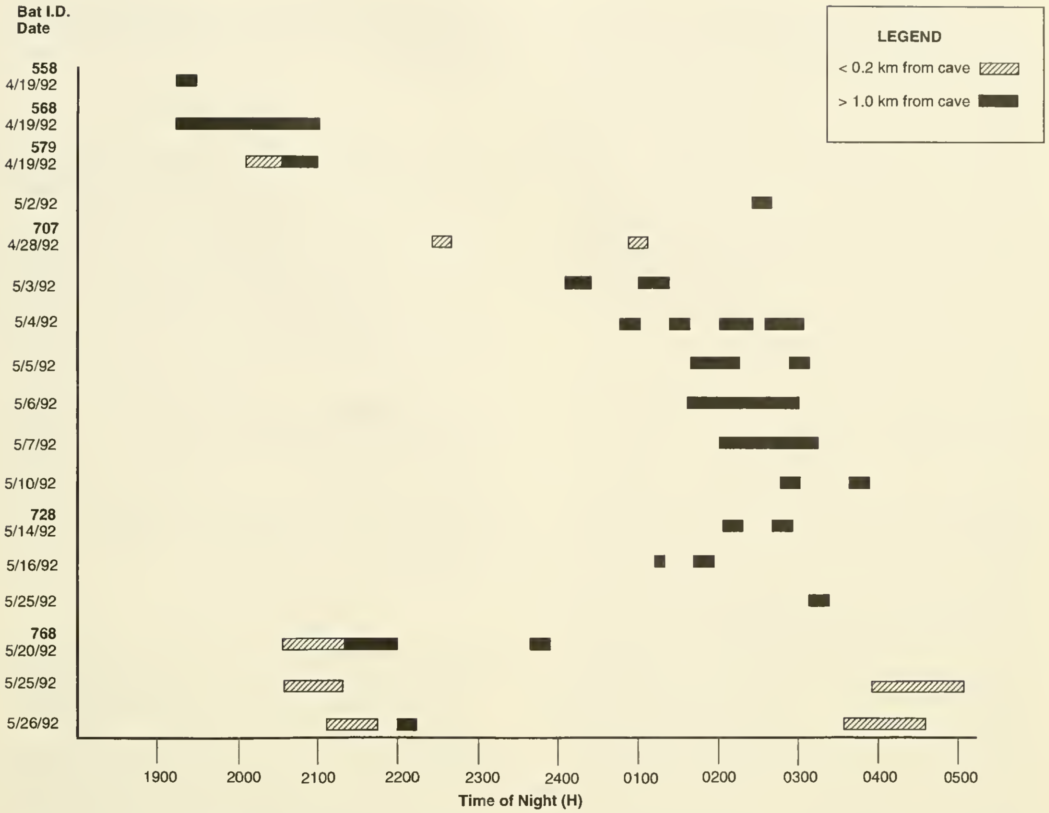

Fig. 2. Temporal distribution (Pacific Daylight Savings Time) of foraging activity by Townsend's big-eared bats in relation to distance from daytime roost sites in forested lava flows of central Oregon.

least the next 12 days. With such small sample sizes, we cannot say whether males and females differ in their use of roosts during this period or whether both sexes exhibit the same pattern of periodic use. We believe that the most reasonable interpretation of the data is that both sexes opportunistically use interim roost sites during this period, and that the choice of roost area is most likely determined by spatial and temporal variation in prey availability. Even species that exhibit strong individual fidelity to day roosts and repeated use of the same foraging areas on successive nights (e.g., *Euderma maculatum*) shift both roost site and foraging area seasonally (Wai-Ping and Fenton 1989).

Big-eared bats in our study moved up to 24 km from hibernacula to foraging areas, although our data suggest that distances moved from interim day roosts to foraging areas are typically 2–8 km during the period prior to entry into maternity colonies. These shorter moves between roosts and foraging areas are consistent with research on eastern subspecies of big-eared bats in which females foraged at distances of 2–7 km from their roosts (Clark et al. 1993, Adam et al. 1994). Repeated use of the same foraging area on successive nights or alternation among several sites appears to characterize both eastern subspecies of big-eared bats (Anonymous 1991, Clark et al. 1993, Adam et al. 1994), as well as big-eared bats in central Oregon (e.g., bat #707).

Although big-eared bat diets are composed primarily of forest Lepidoptera, bats in eastern Oklahoma foraged preferentially at the interface between forested and open pasture habitats (Clark et al. 1993). Nevertheless, bats extensively used open, forest, and edge habitats, and significant shifts in relative habitat use were recorded by Clark et al. (1993). Similarly, in central Oregon we found that Townsend's big-eared bats foraged primarily (but not exclusively) in the more open habitats provided by shrubsteppe and forest-shrub ecotones.

In our study, activity patterns of big-eared bats in spring most closely resembled patterns documented for females of eastern subspecies during late lactation and prior to parturition (Clark et al. 1993, Lacki et al. 1994), i.e., portions of the annual cycle when females are less constrained in the amount of time they can spend away from the maternity cave. Flight initiation inside caves and subsequent emergence documented by Clark et al. (1993) and by Lacki et al. (1994) were identical to the patterns exhibited in our study.

Primary determinants of habitat suitability for Ozark big-eared bats are the availability of an adequate food supply and appropriate roost sites (Clark et al. 1995). Unlike areas where big-eared bats are limited by a small number of suitable roost sites, the extensive forested lava flows found in the Pacific Northwest offer numerous potential temporary roost sites that enable individual bats to forage over a considerable area by using a succession of roost sites during the period following emergence from their hibernaculum. Bats still are limited seasonally, however, to a very small number of sites that provide suitable microclimatic conditions for hibernacula and maternity caves. Such an interpretation of potential movement patterns is consistent with our tracking data and the loss of contact with telemetered bats for successive days followed by subsequent contact. Even our seven attempts to locate bats by aircraft, which should have avoided problems arising from topographic interference with transmitter signals, succeeded only once, indicating that bats may well have left the basin entirely, as was apparently the case for at least the one bat we detected southeast of the study area in the vicinity of the previously unknown maternity cave.

Populations of Townsend's big-eared bats inhabiting regions with extensive lava flows likely use many roost sites dispersed over large areas. The extent of movements that we documented and the use of the same foraging areas by bats from both ends of the basin make it unlikely that bats from southern and northern hibernacula represent separate populations. A better understanding of movements among seasonal and interim roost sites is urgently needed for successful conservation of dwindling populations. Our data demonstrate that the actual area of concern for management of individual populations is considerably greater than indicated solely by locations of hibernacula and maternity caves.

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NAMES AND TYPES IN PERENNIAL *ATRIPLEX* LINNAEUS (CHENOPODIACEAE) IN NORTH AMERICA SELECTIVELY EXCLUSIVE OF MEXICO

Stanley L. Welsh[1] and Clifford Crompton[2]

ABSTRACT.—Cited are names and combinations within the woody species of *Atriplex* as they occur in North America. Types and their repositories are included for all taxa except those for which that information could not be located. New nomenclatural proposals include *Atriplex gardneri* var. *aptera* (A. Nelson) Welsh & Crompton, comb. nov.; *A. garrettii* var. *navajoensis* (C. A. Hanson) Welsh & Crompton, comb. nov.; *Atriplex acanthocarpa* var. *coahuilensis* (Henrickson) Welsh & Crompton, comb. nov. A lectotype is designated for *A. breweri* S. Watson.

Key words: Chenopodiaceae, Atriplex *types, North America.*

This list of names and synonyms of perennial and woody *Atriplex* taxa is preliminary to the preparation of a taxonomic treatment for the woody species of *Atriplex* as they occur in North America, both indigenous and introduced species. All names, whether treated as taxa recognized by me or as mere synonyms, are included. The taxonomic treatment that will appear subsequently in the publication of the Flora North America Project will distinguish between the names of taxa per se and their included synonyms. The relatively large number of names and synonyms for this small group of plants is indicative of the changes in generic concepts, the ever-changing interpretation of the status of a taxon, and the general phenotypic plasticity of this amazing group of shrubs, subshrubs, and perennial herbs, which hybridize freely among themselves and sometimes with other taxa not apparently closely allied. They grow on a surprising array of substrates in the American West, from the cold temperate of northern Alberta to the much warmer climates of Mexico. Often they are among the most important shrub species on saline, fine-textured substrates, and sometimes they are the only shrubby inhabitants. Their ability to survive and even thrive in saline sites has placed them in a position of importance for browsing animals where other browse is scarce or lacking. They cover huge areas where geomorphological processes have exposed raw, saline strata in vast expanses. Niobrara Shale, Mancos Shale, Morrison Formation, and numerous other geological formations support these plants. Saline pans and other poorly drained lowlands are occupied by these species. Despite the affinity for saline areas, where they have little competition (except from other halophytes), some of the species thrive where total soluble salts are low. The four-wing saltbush, *Atriplex canescens* (Pursh) Nuttall, is such a plant. It grows from the edge of saline areas up gradient into far less saline substrates, often in grasslands or in shrublands dominated by sagebrush and other shrubby species.

Hybridization is an important factor contributing to the diversity of woody *Atriplex* species. There are at least two main taxa around which many of the remainder are placed, and with which most form at least occasional hybrids, i.e., *A. canescens* (Pursh) Nuttall and *A. confertifolia* (Torrey & Frémont) S. Watson. Some of the hybrids have received names and formal taxonomic recognition. Most of them are of occasional occurrence, and some of the taxa treated in contemporaneous taxonomic works are apparently of hybrid derivation—now more or less stabilized as populations, mainly on very peculiar substrates.

The following list is thought to be exhaustive for woody and perennial *Atriplex* names in North America, especially for those north of Mexico. A few taxa represented in Mexico are included where they round out the names for species complexes largely confined north of that country. Pertinent types have been received on loan by the gracious kindness of curators of the herbaria cited with the specimens. Abbreviations for the herbaria are those standard ones cited in Index Herbariorum, except that the origin of the collection is indicated by use of such designations as NY Torrey for historic specimens. This is thought to be important because it authenticates the antiquity of the specimen and might prove important in certain cases in judging whether a particular author had access to a given specimen.

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The type information is presented below in dual format for some taxa, with the type locality or collector information (herein arbitrarily designated "Type locality") as recorded with the protologue cited first and with the label data of the type specimen (herein designated "Type") cited second where there is a substantial difference in the two accounts.

***Atriplex acanthocarpa* (Torrey) S. Watson**, Proc. Amer. Acad. Arts 9: 117. 1874.

Basionym: *Obione acanthocarpa* Torrey

This is a shrub or subshrub, generally less than 1 m tall, characterized by spongy fruiting bracteoles 8–15 mm long, borne on slender to stout pedicels 4–20 mm long. Leaves are variable, but often sinuate-dentate to undulate-crisped and with hastately lobed base. The species occurs from west Texas and southern New Mexico south to Mexico. It is represented in the United States by two varieties, i.e., var. *acanthocarpa* from western Texas west through southern New Mexico to southeastern Arizona, and var. *coahuilensis* in southern Texas.

***Atriplex acanthocarpa* ssp. *coahuilensis* Henrickson**, Southw. Naturalist 33: 458. 1988.

= *A. acanthocarpa* var. *coahuilensis* (Henrickson) Welsh & Crompton (cited below).

Type: Mexico, Coahuila, ca 2 km W of Nadadores in saline pastured flats near El Porvinir along Hwy. 30, with Suaeda, Sporobolus, Distichlis, nar 27°03′ N lat, 101°37′W long, 540 m, 6 Dec 1975, J. Henrickson 14784; holotype TEX; isotypes MEXU, NY!, RSA.

This taxon is distinguished by its fruiting bracteoles bearing radiating processes, and stems with at least the medial leaf blades hastate-lanceolate, and with mature fruiting inflorescences very long. Its range is from southern Texas to southeast Coahuila and coastal Tamaulipas.

***Atriplex acanthocarpa* var. *coahuilensis* (Henrickson) Welsh & Crompton**, comb. nov.

Basionym: *A. acanthocarpa* ssp. *coahuilensis* Henrickson, Southwest. Nat. 33: 458. 1988.

***Atriplex acanthocarpa* var. *cuneata* (A. Nelson) M. E. Jones**, Contr. West. Bot. 11: 20. 1903.

= *A. gardneri* var. *cuneata* (A. Nelson) Welsh

***Atriplex acanthocarpa* var. *pringlei* (Standley) Henrickson**, Southwest. Nat. 33: 461. 1988

Basionym: *A. pringlei* Standley

The taxon is endemic to Mexico, from northern Zacatecas and southern Nuevo Leon south to San Luis Potosi.

***Atriplex acanthocarpa* ssp. *stewartii* (I. M. Johnston) Henrickson**, Southwest. Nat. 33: 457. 1988.

Basionym: *A. stewartii* I. M. Johnston

The taxon is endemic to Coahuila, Mexico, and is distinguished by its 4-winged fruiting bracteoles, although specimens are transitional to *A. acanthocarpa* var. *acanthocarpa*.

***Atriplex amnicola* P. G. Wilson**, Flora of Australia 4: 322. 1984.

Type: "Yalgoo, W. A." [western Australia], 10 Oct. 1945, C. A. Gardner 7751a; holotype PERTH!

***Atriplex angustior* Cockerell**, Proc. Davenport Acad. Nat. Sci. 9: 7. 1902.

= *A. canescens* (Pursh) Nuttall

Type: New Mexico, Dona Ana Co., Mesilla Park, Cockerell in 1900; holotype US!

The US specimen bears the following label data: "Atriplex angustior, n. sp. Distinguished from A. canescens by the very narrow (3 mm broad) leaves. Apparently = A. canescens angustifolia but that name is preoccupied. Sand Hills Mesilla Park, N. M. 1900. T.D.A. Cockerell."

Hall and Clements (1923) cited this as a new name for *A. canescens* var. *angustifolia*, but it seems obvious that while Cockerell recognized the equivalency of the taxa, he was proposing a new taxon, not merely a new name.

***Atriplex aptera* A. Nelson**, Bot. Gaz. 34: 356. 1902.

= *A. gardneri* var. *aptera* (A. Nelson) Welsh & Crompton

Type locality: Wyoming, Laramie, Sept. 1901, E. Nelson 738; A. Nelson (1902).

Type: "*Atriplex aptera* A. Nels. n. sp. Moist saline soil. Laramie, Albany Co., Wyoming. Sept. 1901. Elias Nelson No. 738"; holotype RM!; isotype GH!, UC (frag.)!

Hanson (1962) suggested that his taxon was of hybrid derivation involving *A. canescens* and *A. buxifolia* as parental taxa. Distribution of specimens assignable to the concept is sporadic, possibly indicating multiple origins, and it cannot be considered a taxon in the usual sense. The type specimen of *A. aptera* has definite wings aligned in four rows similar to some *A. canescens* but agrees in aspect, size, and general features with *A. gardneri.*

***Atriplex berlandieri* Moquin-Tandon**, Chenop. Enum. 65. 1840.

= *A. canescens* (Pursh) Nuttall

Type: "In regno Mexicano. Berlandier 1828"; holotype ?

Moquin-Tandon enlarges on the type information in his treatment in Prodromus (13[2]: 114. 1849), "In regno Mexicano inter Laverdo et Bejar (Berland.! n. 1450)."

***Atriplex bonnevillensis* C. A. Hanson**, Stud. Syst. Bot. Brigham Young Univ. 1: 2. 1962.

= *A. gardneri* var. *bonnevillensis* (C. A. Hanson) Welsh

Type: Utah, Millard Co., "dry lake bed 1.5 miles northeast of headquarters, Desert Range Experiment Station (dominant plant)," 12 July 1961, C. A. Hanson 354; holotype BRY!; isotypes GH!, MO!, NY!, UTC!

The sheets at GH and NY have the date printed as 13 July 1961, probably representing typographical errors.

Atriplex breweri **S. Watson,** Proc. Amer. Acad. Arts 9: 119. 1874.

Type locality: "Frémont; 459 Torrey; 75 Brewer" (l.c.).

Paratypes: "Frémont's 2nd Expedn. Atriplex Breweri S. Wats."; NY Torrey!; "No. 459. Santa Barbara County, California. J. Torrey, 1865"; NY! and NY LeRoy!, GH!

Type: "Geological Survey of California, 1863. Coll. H. Brewer. No. 75. Atriplex Breweri n. sp. Sea Shore—Sta Monica. 6"[ft] high or more"; lectotype GH!, here designated; isolectotypes NY!, UC, US!

Since the plant was described by Watson on the basis of at least three collections, and as there are duplicates of the Brewer collection, it is proper to designate the material at GH as lectotype. The sheet at US bears a sketch and notes by John Torrey: "75. Obione—near the Sea, at Sta Monica: Probably O. lentiformis (large fruited) in an abnormal state. The bracts appear to have been changed by galls."

Recognition of *A. breweri* at taxonomic level as either a variety or subspecies of *A. lentiformis* is not without merit. Indeed, the plants have typically larger leaves and fruiting bracteoles that average larger. However, there is a series of intermediates that connect the robust coastal material with the less robust plants in the interior. Plants designated as belonging to *A. breweri* are considered by me as taxonomically negligible.

Atriplex buxifolia **Rydberg,** Bull. Torrey Bot. Club 39: 311. 1912.

= *A. gardneri* var. *aptera* (A. Nelson) Welsh

Type locality: Wyoming, Sheridan Co., Dayton, 1220 m altitude, September 1899, Tweedy 2456; holotype NY!

Type: "F. Tweedy 2656 (2456 in publication), Dayton, 4000 ft, Sheridan Co., Wyoming, September 1899"; lectotype NY! (Basset et al. Genus *Atriplex* in Canada 58. 1983).

Atriplex canescens **(Pursh) Nuttall,** Genera N. Amer. Pl. 1: 197. 1818.

Basionym: *Calligonum canescens* Pursh

Putative or actual hybrids are known between *A. canescens* and *A. confertifolia* or *A. gardneri* (various varieties). Such hybrids are only occasional; they do not swamp the characteristics of the taxa nor persist as populations. The two exceptions to the sporadic nature of the hybrids involving *A. canescens* as one of the parental types are *A. gardneri* var. *bonnevillensis* and *A. gardneri* var. *aptera*. Neither of these overwhelms the parental taxa, but being long-lived, they persist for long periods of time and occupy rather large areas in specific habitats. Bracts with four wings appear to have arisen independently at several places within the woody atriplexes. Such a condition is not necessarily an indication of close genetic affinities. Indeed, the *garrettii* and *acanthocarpa* complexes seem to be more distantly removed from *A. canescens* than from other taxa.

Atriplex canescens **var. *angustifolia*** **(Torrey) S. Watson,** Proc. Amer. Acad. Arts 9: 121. 1874.

= *A. canescens* (Pursh) Nuttall

Basionym: *Obione occidentale* var. *angustifolia* Torrey

Narrow-leaved shrubs from west Texas are transitional with broader-leaved materials both there and elsewhere. They do not seem to constitute a taxon.

Atriplex canescens **ssp. *aptera*** **(A. Nelson) Hall & Clements,** Publ. Carnegie Inst. Wash. 326: 343, pl. 58. 1923.

Basionym: *A. aptera* A. Nelson

= *A. gardneri* var. *aptera* (A. Nelson) Welsh

Atriplex canescens **var. *aptera*** **(A. Nelson) C. L. Hitchc.,** Vasc. Pls. Pacif. NW. 2: 186. 1964.

Basionym: *A. aptera* A. Nelson

= *A. gardneri* var. *aptera* (A. Nelson) Welsh

Atriplex canescens **ssp. *garrettii*** **(Rydberg) Hall & Clements,** Publ. Carnegie Inst. Wash. 326: 344. 1923.

Basionym: *A. garrettii* Rydberg

Atriplex canescens **var. *garrettii*** **(Rydberg) Benson,** Amer. J. Bot. 30: 236. 1943.

Basionym: *A. garrettii* Rydberg

Atriplex canescens **var. *gigantea*** **Welsh & Stutz,** Great Basin Nat. 44: 189. 1984.

Type: Utah, Juab Co., Lynndyl sand dunes, T35S, R4W, 8 Sept. 1965, S. L. Welsh & G. Moore 5126; holotype BRY!; isotype NY!

The variety is based on its very broad bracts, stems that produce roots by layering, thus accommodating burial in dunes, and diploid chromosome number.

Atriplex canescens **var. *laciniata*** **Parish,** in Jepson, Fl. Calif. 442. 1914.

= *A. canescens* × *A. polycarpa*? as to possible origin.

Type locality: California, Imperial Co., "Caleb, Colorado Desert, Parish 8256" (Jepson l.c.).

Type: California, Imperial Co., "Plants of Southern California, Salton Basin, Caleb. About 200 feet below sea level. No. 8256. Coll. S. B. Parish. Oct 11. 1911"; holotype UC JEPS!; isotype GH!

This variety has been suggested as based on specimens intermediate between *A. canescens* and *A. linearis* (C. A. Hanson l.c.), although Stutz (personal communication 1994) poses quite another possibility, i.e., that a chromosomal race of *A. polycarpa* forming hybrids with *A. canescens* has resulted in at least partially stabilized populations of var. *laciniata* within the Salton Basin. The type is characterized by deeply laciniate, 4-lobed bracteoles within the size range of *A. canescens*. It has slender branchlets and narrow leaves approaching those of both *A. linearis* and *A. canescens* var. *macilenta*, which had a similar origin from a separate chromosomal race of *A. polycarpa* forming hybrids with *A. canescens*.

Atriplex canescens **ssp. *linearis*** **(S. Watson) Hall & Clements,** Publ. Carnegie Inst. Wash. 326: 344, pl. 58. 1923.

Basionym: *A. linearis* S. Watson

= *A. linearis* S. Watson

Atriplex canescens **var. *linearis*** **(S. Watson) Munz,** Manual S. Calif. Bot. 141. 1935.

Basionym: *A. linearis* S. Watson

= *A. linearis* S. Watson

Atriplex canescens **ssp. *macropoda*** **(Rose & Standley) Hall & Clements,** Phylog. Meth. Taxon 344. 1923.

Basionym: *A. macropoda* Rose & Standley

This taxon is known from Baja California.

Atriplex canescens **var. *macilenta*** **Jepson,** Fl. Calif. 1: 442. 1914.

Type locality: California, Imperial Co., "Holtville, Colorado Desert, Parish 8258" (l.c.).

Type: California, Imperial Co., "Plants of Southern California. Salton Basin. Bluffs of Alamo River, Halbartle. About 15 feet below Sea Level, S. B. Parish 8258, Oct. 18, 1912"; holotype UC JEPS!; isotypes DS ("Calexico"), GH!, POM!

The type has leaves to 4 mm wide, narrowly oblanceolate and obtuse apically. Bracts are small, as in *A. linearis*, and toothed along the margin of the wings. The toothed margin of the wings hints at the laciniate nature of bracts on plants from the nearby Salton Basin and named var. *laciniata* Parish. Plants called var. *macilenta* approach but do not exactly match the more characteristic specimens of *A. linearis* from southern Arizona and northern Mexico. According to Stutz (personal communication 1994), the var. *macilenta* is a high polyploid, while *A. linearis* is a diploid. The relatively broader, thicker leaves of var. *macilenta* are apparently diagnostic.

The specimen at DS, Parish 8258, Oct. 1912, is labeled as having been taken on "Bluffs of the Alamo, Calexico." It is one of three localities cited under Parish's number 8253, and the specimens other than the one taken at Holtville are probably best considered as paratypes.

Parish made a series of collections from the Salton Basin in October 1912. His numbers 8255 and 8256 were collected on October 11; 8255 is a small-bracteoled, narrow-leaved plant assignable to var. *macilenta*, the type of which (8258) was taken on 18 October. Parish's number 8256, the type of var. *laciniata*, is evidently closely placed geographically within the Salton Basin, which also supports *A. polycarpa*, which is potentially involved in the origin of both vars. *macilenta* and *laciniata* through hybridization with different chromosome races of *A. polycarpa* through hybridization with *A. canescens*. Number 8255 approaches *A. linearis* in size of bracts and width of leaves, and possibly that species is also involved in the derivation of both vars. *laciniata* and *macilenta*.

***Atriplex canescens* var. *occidentale* (Torrey & Frémont) Welsh & Stutz,** Great Basin Nat. 44: 188. 1984.

Basionym: *Pterochiton occidentale* Torrey & Frémont

= *A. canescens* (Pursh) Nuttall var. *canescens*

This name was resurrected on false supposition that the type of *A. canescens* sensu stricto differed from the tall phases of the plant so widely distributed in the American West. It is an unfortunate later synonym.

***Atriplex collina* Wooton & Standley,** Contr. U.S. Natl. Herb. 16: 119. 1913.

= *A. confertifolia* (Torrey & Frémont) S. Watson

Type: Arizona, Apache Co., "dry hills near the north end of the Carrizo Mountains," P. C. Standley 7481, 31 July 1911; holotype US!

***Atriplex confertifolia* (Torrey & Frémont) S. Watson,** Proc. Amer. Acad. Arts 9: 119. 1874.

Basionym: *Obione confertifolia* Torrey & Frémont, in Frémont

***Atriplex corrugata* S. Watson,** Bot. Gaz. 16: 341. 1891.

Type locality: "Nearly allied to *A. nuttallii*. Discovered by Miss Alice Eastwood at Grand Junction, Colorado, in well formed fruit on 20th May, 1891. Miss Eastwood notes it as the earliest in fruit of several perennial species of the genus growing in the same locality" (l.c.).

Type: "Atriplex corrugata Watson, n. sp. Grand Junction, Colorado. Miss Alice Eastwood—May 20/1891"; holotype GH!; isotypes UC (fragments taken from holotype by H. M. Hall)!, K, MO, US!

The type consists of two fertile branches, one pistillate and the other staminate. Both have the small, narrow leaves characteristic of the taxon throughout its rather small range. The species is almost exclusively restricted to saline substrates of such fine-textured strata as the members of the Cretaceous Mancos Shale and Jurassic Morrison Formation, inter alia, where it often occurs as a monotype. It forms occasional hybrids with *A. confertifolia* and *A. gardneri* var. *cuneata*, with whom its ecology is sporadic. The taxon is probably most closely allied to the latter, with which it shares large land areas, but from which its autecology is restricted. It is regarded herein at species rank because of the maintenance of morphological integrity despite occasional contact with the other taxa over much of its area. Additionally, there are hints in its morphology of close ties in still another direction, i.e., with *A. obovata*.

***Atriplex cuneata* A. Nelson,** Bot. Gaz. 34: 357. 1902.

= *A. gardneri* var. *cuneata* (A. Nelson) Welsh

Type locality: "M. E. Jones 5443, Emery, Utah, 1894," Nelson (1902).

Type: M. E. Jones 5443, Emery, 7000 ft., Emery Co., Utah, 16 June 1894; holotype RM!; isotypes MO!, NY! (3 sheets), US!

***Atriplex cuneata* ssp. *introgressa* C. A. Hanson,** Stud. Syst. Bot. Brigham Young Univ. 1: 4. 1962.

= *A. gardneri* var. *cuneata* × var. *tridentata*

Type: Utah, Carbon Co., "Wellington, ca 0.1 mi S of Price River, in clay hills along road leading to city dump," 9 July 1961, Hanson 346; holotype BRY!; isotypes GH!, POM!

The specimens on which this taxon are based demonstrate intermediacy between the *cuneata* and *tridentata* phases of *A. gardneri*. Their recognition at any taxonomic level is problematical.

***Atriplex curvidens* T. S. Brandegee,** Proc. Calif. Acad. Sci. II, 2: 201. 1889.

= *A. polycarpa* (Torrey) Watson

Type: Baja California, Comondu, four feet high, rounded April 24, 1889, Brandegee sn; holotype UC!

***Atriplex decumbens* S. Watson,** Proc. Amer. Acad. Arts 12: 275. 1877.

= *A. watsonii* A. Nelson.

Type locality: California, "Near San Diego; Dr. E. Palmer, 1875 (n. 334)" (Watson 1877).

Type: "Southern part of San Diego Co., California. Coll. Edward Palmer, M.D., 1875. No. 334. Atriplex decumbens, Watson n. sp. San Diego"; holotype GH!; isotype NY! (2 sheets).

The type consists of a small and a large branch, both staminate. The large branch is evidently from a sprawling herbaceous perennial. Leaves are mostly opposite, becoming subopposite above, elliptic to ovate-lanceolate, obtuse to rounded apically; the glomerules are 3–5 mm thick and are arranged in terminal spikes 1–4 cm long.

***Atriplex eremicola* Osterhout,** Bull. Torrey Bot. Club 25: 284. 1898a. nom. nov.

Basionym: *A. fruticulosa* Osterhout.

= *A. gardneri* (Moquin-Tandon) Dietrich var. *gardneri*

Atriplex falcata **(M. E. Jones) Standley,** N. Amer. Fl. 21: 68. 1916.

Basionym: *A. nuttallii* var. *falcata* M. E. Jones, Contr. W. Bot. 11: 19. 1903.

= *A. gardneri* var. *falcata* (M. E. Jones) Welsh

Atriplex fruticosa **Nuttall ex Moquin-Tandon,** in de Candolle, Prodr. 13(2): 112. 1849. pro syn.

= *A. gardneri* var. *gardneri*

Type: "*Atriplex* * *fruticosa.* A. Halimum affinis. R. Mts." Nuttall; holotype BM!

The type of *A. fruticosa* is mounted with collections with the notation "British North America. Dr. Richardson 1819–28," and designated as *A. canescens.* In Index Kewensis the name *fruticosa* is noted as a synonym of *A. canescens,* a supposition possibly based on the identity of the Richardson material, but more probably on the publication of the name as a synonym of *A. canescens* by Moquin-Tandon. The epithets *fruticosa* and *heterophylla,* both herbarium names of Nuttall, were published as synonyms and are not to be regarded in considerations of priority.

Atriplex fruticulosa **Jepson,** Pittonia 2: 306. 1892.

Type: California, "Little Oak, Solano Co., Aug. 16, 1892. Willis L. Jepson"; holotype UC!; isotype MO!

This plant functions mostly as an annual but is apparently capable of a longer life span, extending to become a short-lived perennial. The name has priority over the later homonym, *A. fruticulosa* Osterhout (1898).

Atriplex fruticulosa **Osterhout,** Bull. Torrey Bot. Club 25: 207. 1898. non *A. fruticulosa* Jepson 1892.

Basionym for: *A. eremicola* Osterhout

= *A. gardneri* (Moquin-Tandon) Dietrich var. *gardneri*

Type locality: Wyoming, Albany Co., Steamboat Lake, "The type was collected near a small alkaline lake in Southern Wyoming," G. Osterhout s.n. 2 July 1896; holotype (no. 1324) RM!; isotype NY!, RM! (this second sheet, presumably an isotype, lacks the collector's number). A collector's number was not cited with the protologue, but the holotype sheet at RM bears the number 1324. Material on which this entity was based differs in no particular way from *A. gardneri* var. *gardneri.*

Atriplex gardneri **(Moquin-Tandon) Dietrich,** Syn. Pl. 5: 537. 1852.

Basionym: *Obione gardneri* Moquin-Tandon

There is a sheet, possibly identifiable as belonging to this species and not bearing on the nomenclature of the species, in the Lewis and Clark herbarium at PH: "A half shrub from the high plains of Missouri. July 20th 1806." It is cited here to demonstrate that the species was known from the earliest collections into the western plains.

Atriplex gardneri **var. *aptera*** **(A. Nelson) Welsh & Crompton,** comb. nov.

Basionym: *Atriplex aptera* A. Nelson, Bot. Gaz. 34: 356. 1902.

This entity was treated by Hanson (1962) as a probable derivative of hybridization between *A. canescens* and *A. buxifolia* (*A. gardneri* sens. lat.). It is a low subshrub most similar to the latter, but with bracteoles winged as in *A. canescens* or with tubercles aligned in four rows, and with yellow staminate flowers. It is likely that the condition of 4-winged fruits has arisen independently on many occasions and that the resulting populations are not associated genetically as in a typical taxon. Regardless of origin, however, the resultant plants are readily recognizable and are widely distributed from southern Canada south along the plains to Nebraska and Wyoming. *A. canescens* also forms hybrids with other phases of the *gardneri* complex (see below).

Atriplex gardneri **var. *bonnevillensis*** **(C. A. Hanson) Welsh,** Great Basin Nat. 44: 190. 1984.

Basionym: *A. bonnevillensis* C. A. Hanson

This variety is more or less intermediate between *A. gardneri* var. *falcata* and *A. canescens,* but it most nearly resembles the former in habit. The bracteoles are 5–8 mm long and 3–9 mm wide, ovoid, with four lateral wings or rows of flattened tubercules to 3 mm wide, or the wings rarely absent. The plants are confined to playas and saline pans in the valleys of western Utah and across Nevada.

Atriplex gardneri **var. *cuneata*** **(A. Nelson) Welsh,** Great Basin Nat. 44: 191. 1984.

Basionym: *A. cuneata* A. Nelson

Atriplex gardneri **var. *falcata*** **(M. E. Jones) Welsh,** Great Basin Nat. 44: 191. 1984.

Basionym: *A. nuttallii* var. *falcata* M. E. Jones

Atriplex gardneri **var. *tridentata*** **(Kuntze) Macbride,** Contr. Gray Herb. 3: 11. 1918.

= *A. gardneri* var. *utahensis* (M. E. Jones) Dorn

Basionym: *A. tridentata* Kuntze

Atriplex gardneri **var. *welshii*** **(C. A. Hanson) Welsh,** Great Basin Nat. 44: 191. 1984.

Basionym: *A. welshii* C. A. Hanson

Atriplex gardneri **var. *utahensis*** **(M. E. Jones) Dorn,** Vasc. Pl. Wyo. 130. 1988.

Basionym: *A. nuttallii* var. *utahensis* M. E. Jones

Atriplex garrettii **Rydberg,** Bull. Torrey Bot. Club 39: 312. 1912.

Type: Utah, Grand Co., "Vicinity of Moab," July 1–2, 1911, P. A. Rydberg & A. O. Garrett 8465; holotype NY!; isotypes GH!, US!, UT!

Despite earlier treatments in which this taxon was regarded at infraspecific status within *A. canescens,* the nearest allies appear to be in the *gardneri* complex. Apparent hybrids are known between *A. garrettii* and *A. confertifolia* (C. A. Hanson 1962), but not with *A. canescens.*

Atriplex garrettii **var. *navajoensis*** **(C. A. Hanson) Welsh & Crompton,** comb. nov.

Basionym: *A. navajoensis* C. A. Hanson, Stud. Syst. Bot. Brigham Young Univ. 1: 3. 1962.

This variety differs from the type material in plant size, length of staminate inflorescences, color of staminate flowers, and other intangibles. Generally the plants are very similar. The few known localities, from the vicinity of Lee's Ferry to Navajo Bridge in Coconino County, AZ, are only disjunct by about 100 km from the nearest populations of var. *garrettii.*

Atriplex gordoni **Hooker,** J. Bot. 5: 261. 1853. nom. nov. pro *A. gardneri* Moquin-Tandon.

= *A. gardneri* (Moquin-Tandon) Dietrich var. *gardneri*

Atriplex greggii **S. Watson,** Proc. Amer. Acad. Arts 9: 118. 1874.

= *A. obovata* Moquin-Tandon

Type locality: "New Mexico to Sonora. Collectors:—1346 Berlandier; 462 Gregg; Emory; Thurber; Bigelow; 572, 1137, 1138 Wright" (Watson l.c.).

Paratypes: "No. 462. Atriplex obovata Moq. Perros Bravos, Coahuila, Mexico, Dr. J. Gregg, leg. 1848–49" (GH Lowell!); "Berlandier, No. 1346. Bae de del Salad, San Luis Potosi, 1827" (GH!).

Type: "462. Atriplex. *Perros Bravos*, north of Saltillo. 1 ft. tall. Abundant. *State of Coahuila*, Mexico. Dr. J. Gregg, leg. Sept. 20, 1848"; lectotype GH! (I. M. Johnston, J. Arnold Arb. 25(2): 147. 1944); isolectotype GH Lowell!

***Atriplex griffithsii* Standley**, N. Amer. Fl. 21: 63. 1916.

= *A. lentiformis* var. *griffithsii* (Standley) L. Benson

Type: Arizona, Cochise Co.: "Wilcox," Griffiths sn. 1895, Oct. 12, 1900; holotype NY!; isotype US!

This is a distinctive taxon with silvery, thick leaves. It is disjunct from the remainder of the species.

***Atriplex heterophylla* Nuttall ex Moquin-Tandon**, in de Candolle, Prodr. 13(2): 112. 1849. pro syn.

= *A. gardneri* (Moquin-Tandon) Dietrich var. *gardneri*

Type: "Atriplex * *heterophylla*. R. Mts." Nuttall; intended type BM!

This is yet another herbarium name by Nuttall cited as a synomym of *A. canescens* by Moquin-Tandon in de Candolle's Prodromus. It again demonstrates that the species was well represented in collections prior to the collection of the type material of *A. gardneri*.

***Atriplex hymenelytra* (Torrey) S. Watson**, Proc. Amer. Acad. Arts 9: 119. 1874.

Basionym: *Obione hymenelytra* Torrey

***Atriplex johnstonii* C. B. Wolf**, Occas. Pap. Rancho Santa Ana Bot. Gard. 1: 3. 1935.

= *A. nummularia* Lindl.

Type: California, Los Angeles County, Coastal cliffs, Playa del Rey. C. B. Wolf 1821, 23 Dec. 1930; isotypes CAS!, GH!, NY!

The isotype at GH consists of four woody, leafy branches, two of them with fruiting bracts. Leaves are short-petiolate, with blades 1.2–3.5 cm long and 1–3 cm wide.

***Atriplex jonesii* Standley**, N. Amer. Fl. 21: 65. 1916. nom. nov. pro *A. sabulosa* M. E. Jones.

= *A. obovata* Moquin-Tandon

***Atriplex lentiformis* (Torrey) S. Watson**, Proc. Amer. Acad. Arts 9: 118. 1874.

Basionym: *Obione lentiformis* Torrey, in Sitgreaves

This is a warm-desert species, important in saline pans along drainages at low elevations in the valleys of the Colorado and Gila rivers and Salton Sink. The species is distributed from western and southern Arizona, through southern Nevada and California, and also in Mexico. Hanson (1962) notes that *A. lentiformis* sens. lat. forms hybrids with *A. leucophylla* (Moquin-Tandon) Dietrich, a perennial not especially woody species, and possibly even with an annual species. Such hybridizations might indicate that *A. lentiformis* and its near relative *A. torreyi* have alliances elsewhere than with the other woody species treated herein.

***Atriplex lentiformis* ssp. *breweri* (S. Watson) Hall & Clements**, Publ. Carnegie Inst. Wash. 326: 335, pl. 54. 1923.

Basionym: *A. breweri* S. Watson

= *A. lentiformis* sens lat?

***Atriplex lentiformis* var. *breweri* (S. Watson) McMinn**, Man. Calif. Shrubs 113. 1939.

Basionym: *A. breweri* S. Watson

= *A. lentiformis* sens lat?

***Atriplex lentiformis* ssp. *griffithsii* (Standley) Hall & Clements**, Publ. Carnegie Inst. Wash. 326: 336, pl. 55. 1923.

Basionym: *A. griffithsii* Standley

= *A. lentiformis* sens. lat?

***Atriplex lentiformis* var. *griffithsii* (Standley) Benson**, Amer. J. Bot. 30: 236. 1943.

Basionym: *A. griffithsii* Standley

= *A. lentiformis* sens. lat?

***Atriplex lentiformis* ssp. *torreyi* (S. Watson) Hall & Clements**, Publ. Carnegie Inst. Wash. 326: 335. 1923.

Basionym: *Obione torreyi* S. Watson

***Atriplex lentiformis* var. *torreyi* (S. Watson) McMinn**, Man. Calif. Shrubs 113. 1939.

Basionym: *Obione torreyi* S. Watson

***Atriplex linearis* S. Watson**, Proc. Amer. Acad. Arts 24: 72. 1889.

Type locality: Mexico, Sonora, alkaline soil about Guaymas, Palmer 120, 121, 235; syntypes GH.

Paratypes: "Flora of Guaymas, Mex. Dr. Edward Palmer, 1887. No. 120. Atriplex linearis Watson, n. sp. Garden fences in alkaline soil. July"; GH! and "Flora of Guaymas, Mex. Dr. Edward Palmer, 1887. No. 121. Atriplex Linearis, Watson, n. sp. Garden fences, alkaline soil. July"; GH!

Type: "Flora of Guaymas, Mex. Dr. Edward Palmer, 1887. No. 235. Atriplex linearis Watson, n. sp. Plains in alkaline soil. Sept."; lectotype GH! (G. D. Brown, Amer. Midl. Nat. 55: 210. 1956).

Paratypes 120 and 121 are immature, the former pistillate, the latter staminate. The lectotype sheet #235 has at least four branches with more or less mature fruiting bracteoles. The bracteoles are 4-winged, rather deeply laciniately lobed to merely toothed along the wings, and are 3–6 mm wide.

Hanson (1962) regarded *A. linearis* as the most substantial variant within the *canescens* complex but recognized that it forms hybrids with *A. canescens*. The plants are certainly morphologically distinct from most phases of that entity. The slender, short to elongate leaves (seldom more than 4 mm wide and to 3.8 cm long), fruiting bractoles seldom over 6 or 7 mm wide, and very slender branchlets are apparently diagnostic in most instances.

***Atriplex macropoda* Rose & Standley**, N. Amer. Fl. 21: 72. 1916.

= *A. linearis* S. Watson (sens lat?, but the fruiting bracteoles are long pedicellate, unlike *A. canescens*)

Type locality: "Type collected on Pinchillinque Island, Lower California, March 27, 1911, J. N. Rose 16518 (U.S. Nat. Herb. no. 638567)."

Type: Lower California, Pinchilinque Island, Gulf of California, J. N. Rose 16518, March 27, 1911; holotype US!

***Atriplex matamorensis* A. Nelson**, Proc. Biol. Soc. Wash. 17: 99. 1904.

Nom. nov. pro. *A. oppositifolia* S. Watson

Atriplex navajoensis **C. A. Hanson,** Stud. Syst. Bot. Brigham Young Univ. 1: 3. 1962.

= *A. garrettii* var. *navajoensis* (C. A. Hanson) Welsh & Crompton

Type: "Arizona: Coconino Co., east side of the Navajo Bridge, July 21, 1961," C. A. Hanson 388; holotype BRY!; isotype GH!

Atriplex* × *neomexicana **Standley,** N. Amer. Fl. 21: 67. 1916.

= *A. gardneri* var. *cuneata* × *A. confertifolia*

Type locality: "Type collected on dry hills near Farmington, New Mexico, altitude 1550–1650 m, July 19, 1911, Paul C. Standley 7066 (U.S. Nat. Herb. no. 686089)."

Type: New Mexico, "Dry hills near Farmington," San Juan Co., New Mexico, July 19, 1911, P. C. Standley 7066; holotype US!

The name is evidently based on plants intermediate between *A. gardneri* var. *cuneata* and *A. confertifolia*.

Atriplex nummularia **Lindley,** Mitch. J. Exped. Trop. Australia 64. 1848.

Type: Australia, "Cultivated in Italy, seed from South Australia"; holotype not seen.

Atriplex nuttallii **S. Watson,** Proc. Amer. Acad. Arts 9: 116. 1874. nom. nov.

= *A. canescens* (Pursh) Nuttall sens. str.

It is unfortunate that one must at this late date attempt to analyze Watson's use of the name *nuttallii* for a portion of the woody atriplexes in the American West. From its publication in 1874 the name has been the source of much confusion, serving to clutter *Atriplex* nomenclature for all subsequent time. It seems certain from a study of Watson's proposal, justification for which can only be inferred, that he was merely presenting a new name for material that he thought to be misinterpreted by contemporary botanists. The evolution of botanical thought with regard to the perennial atriplex species parallels that for other newly discovered taxa in the American West and was initiated when the first of the woody specimens arrived from western botanical explorers. Few names were available, specimens were few and often fragmentary, literature was difficult to obtain, and it was easy to misapply concepts and mix names, a symptomology not of that era alone.

Supposed sensu names cited by Watson (1874) within the synomymy of *A. nuttallii* include *Atriplex canescens* as used by Nuttall and an assortment of other historical authors, *Obione canescens* of Moquin-Tandon and other authors, and still another synonym, i.e., "*A. gordonii* Hook.," with the citation "Pl. Geyer in Lond. Jour. Bot. 5: 261?," and by implication the type of *A. gordonii* (i.e., *A. gardneri*).

Watson first cited the name *A. canescens* as published by Nuttall (1818), the implication being that *Calligonum canescens* Pursh, basionym of *A. canescens*, could not apply. Nuttall is indeed author of the combination *Atriplex canescens*, and the place of citation is his 1818 publication, wherein he cites *C. canescens* as the basionym of his combination; furthermore, Nuttall's description is clearly *C. canescens* Pursh, sensu stricto. It is Watson's understanding of Nuttall's use of the epithet that is in error. Thus, *A. canescens* of Nuttall is certainly not a mere sensu name, however one might wish to interpret the application of the epithet. Both the name and the concept as supplied by Nuttall are *A. canescens*, including its basionym. *A. nuttallii* of Watson thus includes the type of *Calligonum canescens*, and the epithet *nuttallii* is illegitimate under stipulations of the International Code. Hence, from a nomenclatural viewpoint there is no problem. Nuttall based his *Atriplex canescens* squarely on *Calligonum canescens* Pursh, and Watson quoted *A. canescens* Nuttall as the name-bringing synonym of *A. nuttallii*, which was stillborn. The lectotype of *Caligonum canescens* Pursh is at PH and is therefore the lectotype of both *Obione canescens* and *A. nuttallii*, which cannot be transferred to a different species or brought to life by sophisticated arguments. Hence, the proposal for lectotypification by McNeill et al. (1983) is illegitimate.

Atriplex nuttallii var. ***anomala*** **M. E. Jones,** Contr. W. Bot. 11: 19. 1903.

= *A. gardneri* var. *falcata* (M. E. Jones) Welsh

Type locality: "The type is my specimens from Dolly Varden Smelter, E. Nevada, July 1894 [1891]."

Type: Nevada, Elko Co., "Marcus E. Jones Herbarium. Atriplex nuttallii var. anomata [sic] Jones n. var. Dolly Varden at the Smelter, VII-24-91. N.W. of Ibapah, Utah." M. E. Jones sn; holotype POM!; isotype UC (frag.)!

Jones was clearly in error in citing the date of the collection as 1894. His itinerary cited in Leaflets of Western Botany (10: 189–236) places him at the Dolly Varden Smelter on 24 July 1891, not 1894.

Atriplex nuttallii ssp. ***buxifolia*** **(Rydberg) Hall & Clements,** Phylog. Meth. Taxon. 325. 1923.

Basionym: *A. buxifolia* Rydberg

= *A. gardneri* (Moquin-Tandon) Dietrich var. *gardneri*

Atriplex nuttallii corrugata **(S. Watson) A. Nelson,** in Coulter & Nelson, New. Man. Bot. Rocky Mts. 168. 1909.

= *A. corrugata* S. Watson

Atriplex nuttallii ssp. ***cuneata*** **(A. Nelson) Hall & Clements,** Publ. Carnegie Inst. Wash. 326: 324, f. 45. 1923.

Basionym: *A. cuneata* A. Nelson

= *A. gardneri* var. *cuneata* (A. Nelson) Welsh

Atriplex nuttallii ssp. ***falcata*** **(M. E. Jones) Hall & Clements,** Publ. Carnegie Inst. Wash. 326: 324. f. 45. 1923.

Basionym: *A. nuttallii* var. *falcata* M. E. Jones

= *A. gardneri* var. *falcata* (M. E. Jones) Welsh

Atriplex nuttallii var. ***falcata*** **M. E. Jones,** Contr. W. Bot. 11: 19. 1903.

= *A. gardneri* var. *falcata* (M. E. Jones) Welsh

Type locality: "Weiser, Idaho, July, 1899, Jones" (l.c.).

Type: Idaho, Washington Co., "Flora of Idaho. Type material. Atriplex nuttallii var. falcata Jones n. var. Weiser, Wash. Co. July 7 1899. Alt. 2200 Ft." M. E. Jones sn; holotype POM!; isotype UC!

Atriplex nuttallii ssp. ***gardneri*** **(Moquin-Tandon) Hall & Clements,** Publ. Carnegie Inst. Wash. 326: 324. 1923.

= *A. gardneri* (Moquin-Tandon) Dietrich var. *gardneri*

Basionym: *Obione gardneri* Moquin-Tandon

Atriplex nuttallii ssp. ***tridentata*** **(Kuntze) Hall & Clements,** Publ. Carnegie Inst. Wash. 326: 324. 1923.

= *A. gardneri* var. *utahensis* (M. E. Jones) Dorn

Basionym: *A. tridentata* Kuntze

Atriplex nuttallii var. ***gardneri*** **(Moquin-Tandon) R. J. Davis,** Fl. Idaho. 261. 1952.

= *A. gardneri* (Moquin-Tandon) Dietrich var. *gardneri*
Basionym: *Obione gardneri* Moquin-Tandon

***Atriplex nuttallii* var. *tridentata* (Kuntze) R. J. Davis**, Fl. Idaho 261. 1952.

= *A. gardneri* var. *utahensis* (M. E. Jones) Dorn
Basionym: *A. tridentata* Kuntze

***Atriplex nuttallii* var. *utahensis* M. E. Jones**, Contr. W. Bot. 11: 19. 1903.

= *A. gardneri* var. *utahensis* (M. E. Jones) Dorn

Type locality: "This is No. 1760 Jones from Salt Lake City, and is the more common form in Utah."

Type: Utah, Salt Lake City, Salt Lake Co., M. E. Jones 1760, 16 June 1894; holotype POM?; isotype UC (frag.)!

***Atriplex oblanceolata* Rydberg**, Bull. Torrey Bot. Club 31: 403. 1904.

= *A. gardneri* var. *cuneata* (A. Nelson) Welsh

Type locality: Colorado, Delta Co., Delta, Cowen 4071 (Rydberg 1904).

Type: "Plants of Colorado. No. 4071. Atriplex oblanceolata Rydb. Delta, J. H. Cowen. Sept 3, 1897"; holotype NY!; isotypes GH!, RM! (2 sheets), US!

***Atriplex obovata* Moquin-Tandon**, Chenop. Enum. 61. 1840.

Type locality: "In Peruvia. (v. s. in herb. Mus. Paris)" (l.c.).

Type: "No. 1346. Bae del Salad, Saint Louis Potosi. Dbre. 1827," and "Herbarium Berlandierianum Texano-mexicanum. No. 1346. Atriplex obovata, Moq.! O. canescens, var? Torr. San Luis Potosi; Mexico, State of San Luis Potosi, Berlandier 1346"; lectotype P? (I. M. Johnston, J. Arnold Arbor. 25[2]: 148. 1944); isolectotype GH!

The isolectotype sheet at GH consists of three leafy branches, now lacking fruiting bracteoles or staminate flowers. The material is certainly a match for what has traditionally passed under the name *obovata*; hence, there is no problem with its interpretation.

***Atriplex obovata* var. *tuberata* Macbride**, Contr. Gray Herb. 3: 11. 1918.

= *A. obovata* Moquin-Tandon

Type locality: Texas, El Paso Co., Fornillo Creek, Harberd 103.

Type: "No. 103 (see specimen of male). 1–2° [feet] high —Foliage & specially fruit different from that of A. acanthocarpa. Tornillo Creek. W. Texas. Aug. [18]83. V. Havard, U.S.A."; holotype GH!; isotype US!

The sheet at GH has two branches, one staminate and one with fruiting bracteoles. The bracteoles are rather strongly tuberculate, a feature not unusual within the species as a whole.

***Atriplex occidentalis* (Torrey & Frémont) Dietrich**, Syn. Pl. 5: 537. 1852.

Basionym: *Pterochiton occidentale* Torrey & Frémont
= *A. canescens* (Pursh) Nuttall

***Atriplex odontoptera* Rydberg**, Bull. Torrey Bot. Club 31: 404. 1904.

= *A. canescens* × *A. gardneri* var. *gardneri*

Type: Wyoming, Johnson Co., "3302. *Atriplex canescens* (Pursh) James. A. odontoptera Rydb. (Type) Buffalo. Elevation 4000–5000 feet. Frank Tweedy. September 1900"; holotype NY!; isotype RM!

This is a coarse specimen, very woody and obviously intermediate between *A. canescens* and *A. gardneri* var. *gardneri*

***Atriplex oppositifolia* S. Watson**, Proc. Amer. Acad. Arts 9: 118. 1874, non DC.

= *A. matamorensis* A. Nelson; *Obione oppositifolia* (S. Watson) Ulbrich, in Engler & Prantl

Type locality: "In the Rio Grande Valley on the Mexican side, collected only by Berlandier (No. 3201, 'Matamoras to San Fernando')" (Watson l.c.).

Type: "de Matamaras a San Fernando circa Guijano, Oct. 1830," and "Herbarium Berlandierianum Texano-Mexicanum. No. 3201. A. oppositifolia n. sp. S.W.! [initials are Sereno Watson's on sheet at GH]," Berlandier; holotype GH!; isotype NY!

The specimen at GH is doubly mounted with Palmer 1160, 1879. It is a portion of a herbaceous perennial with minute leaves ca 2–3 mm long and 1 mm wide. Bracteoles are conspicuously veined on the faces and prominently toothed lateral to the apical tooth.

***Atriplex orbicularis* S. Watson**, Proc. Amer. Acad. Arts 17: 377. 1882.

= *A. lentiformis* (Torrey) S. Watson (the *A. breweri* S. Watson phase)

Type locality: "At Santa Monica, California, on the seashore at the base of the bluffs; S. B. & W. F. Parish, October, 1881" (Watson 1882).

Type: "Flora of Southern California, S. B. & F. W. Parish, No. 1126, perennial, somewhat woody at base, 3–4 ft high, base of bluffs, sea shore, Sta Monica, Oct. 1881"; holotype GH!; isotypes DS!, NY!, US!

The fruiting bracts are ca 3 mm high and 4 mm wide. Leaves are elliptical and obtuse, tapering basally to a short petiole.

***Atriplex pabularis* A. Nelson**, Bull. Torrey Bot. Club 25: 203. 1898.

= *A. gardneri* var. *utahensis* (M. E. Jones) Dorn

Type locality: Wyoming, Sweetwater Co., Point of Rocks, A. Nelson 4429, Aug. 30, 1897.

Type: "A. Nelson 4429, Bitter Cr., Point of Rocks, 6500 ft, Sweetwater Co., Wyoming, 30 August 1897"; lectotype at RM! (Hall & Clements, Publ. Carnegie Inst. Wash. 326: 324. 1923); isolectotypes GH! (two sheets, male and female), NY!, US!

***Atriplex pabularis* var. *eremicola* (Osterhout) A. Nelson**, Coulter & Nelson, New Man. Bot. Rocky Mts. 168. 1909.

Basionym: *A. eremicola* Osterhout
= *A. gardneri* (Moquin-Tandon) Dietrich var. *gardneri*

***Atriplex parryi* S. Watson**, Proc. Amer. Acad. Arts 17: 378. 1882.

Type locality: "Near Colton [actually at Lancaster according to Parish in Zoe 5: 113, 1901], California; Dr. C. C. Parry 1881"; holotype (Parry 221) GH!; isotypes NY!, UC (frag.)!

The type consists of a branched stem, with lateral spinescent stems to 4 cm long. The leaves are ovate-orbicular. The plant is obviously allied to *A. confertifolia*, but distinct.

***Atriplex polycarpa* (Torrey) S. Watson**, Proc. Amer. Acad. Arts 9: 117. 1874.

Basionym: *Obione polycarpa* Torrey

***Atriplex pringlei* Standley**, N. Amer. Flora 21: 68. 1916.

= *A. acanthocarpa* ssp. *pringlei* (Standley) Henrickson

Type locality: "Type collected on alkaline plains, Hacienda de Angostura, San Luis Potosi, Mexico, July 15, 1891, C. G. Pringle 3775 (U.S. Nat. Herb. no. 48298)."

Type: "Mexico, San Luis Potosi, alkaline plain, Hacienda de Angostura, 15 Jul 1891," C. G. Pringle 3775; holotype US!; isotype GH!

***Atriplex sabulosa* M. E. Jones**, Contr. W. Bot. 11: 21. 1903. non *A. sabulosa* Rouy, 1890.

Basionym of: *A. jonesii* Standley

= *A. obovata* Moquin-Tandon

Type locality: Arizona, Navajo Co., "No. 4109 Jones, Winslow, Ariz., Sept., 1884, distributed as *A. Greggii*" (Jones 1903).

Type: "Flora of Arizona. 4109. Atriplex Greggii, Watson. Winslow, M. E. Jones, September 1, 1884"; holotype US!; isotypes GH!, NY!, POM!

The isotype at GH consists of three branches, two staminate and one pistillate.

***Atriplex spinifera* Macbride**, Contr. Gray Herb. 53: 11. 1918.

Type locality: California, Kern Co., Maricopa Hills, May 15, 1913, Eastwood 3269 (Macbride 1918).

Type: "3269. Flora of California. Atriplex. Marcopa hills, Kern Co., Alice Eastwood May 15, 1913"; holotype GH!; isotype CAS!, US!

The holotype at GH consists of a branched stem bearing lateral spinescent branches to 4.2 cm long; that at US consists of spinose branchlets and two packets of fruiting bracteoles.

***Atriplex spinosa* (Moquin-Tandon) D. Dietrich**, Syn. Pl. 5: 536. 1852.

Basionym: *Obione spinosa* Moquin-Tandon, in de Candolle

= *A. canescens* (Pursh) Nuttall

***Atriplex stewartii* I. M. Johnston**, J. Arnold Arbor. 22: 110. 1941.

= *A. acanthocarpa* ssp. *stewartii* (I. M. Johnston) Henrickson

Type locality: Mexico.

Type: "Mexico: western Coahuila. Atriplex stewartii n. sp. Jour Arn. Arb. 22: 110. 1941. Eastern border of the Llano de Guaje, along road from Tanque del Aparejo 20 miles southeast of Tanque Armendais. Abundant on flats margining playa at base of Lomas del Aparego (3 miles south of Tangue Asparejo). Plant erect, 10–15 inches tall. I. M. Johnston, C. H. Muller No. 777. Aug. 28, 1940"; holotype GH!

The plant is obviously allied to *A. anthocarpa*, the variably 4-winged fruiting bracteoles having been derived independently or possibly through introgression from *A. canescens*. Henrickson (1988) does not suggest the latter possibility but does note that the 4-winged condition is not consistent, that there is a transition from that condition to those where the wings are replaced by radiating processes.

***Atriplex subconferta* Rydberg**, Fl. Rocky Mts. 248. 1917 [1918].

= *A. confertifolia* (Torrey & Frémont) S. Watson

Type locality: Idaho, between Twin and Shoshone Falls, Nelson & Macbride 1379; holotype NY; isotypes POM, UC.

Type: "No. 1379. Atriplex confertifolia (Torr.) Wats. Dry bench lands, alt. 3700. Twin Falls and Shoshone Falls, 3700 ft., Idaho, July 27, 1911, Aven Nelson & J. F. Macbride"; holotype NY!; isotypes GH!, MO!, POM, RM!, UC, US!

This appears to be a small-leaved phase of *A. confertifolia* of little or no taxonomic significance.

***Atriplex tetraptera* (Bentham) Rydberg**, Bull. Torrey Bot. Club 39: 311. 1912.

Basionym: *Obione tetraptera* Bentham

= *A. canescens* (Pursh) Nuttall

***Atriplex torreyi* (S. Watson) S. Watson**, Proc. Amer. Acad. Arts 9: 119. 1874.

Basionym: *Obione torreyi* S. Watson

***Atriplex torreyi* var. *griffithsii* (Standley) G. D. Brown**, Amer. Midl. Nat. 55: 205. 1956.

Basionym: *A. griffithsii* Standley

= *A. lentiformis* (Torrey) S. Watson

***Atriplex tridentata* Kuntze**, Rev. Gen. Pl. 2: 546. 1891.

= *A. gardneri* var. *utahensis* (M. E. Jones) Dorn

Type locality: Utah, Box Elder Co., Corrine, Kuntze 3084, 1874.

Type: O. Kuntze 3084, "Bei Corinne am Salzsee, 7000 [much too high] ft, [Box Elder Co.], Utah, September 1874"; holotype NY!; isotype? K!

The specimen at K, labeled "Atriplex tridentata OKze n. sp. U.S. N. Am. zw. Cheyenne & Corinne. 7000′. Sept. 74. 3084. Herbarium Otto Kuntze," is perhaps best regarded as a paratype.

***Atriplex watsonii* A. Nelson**, Proc. Biol. Soc. Wash. 17: 99. 1904. nom. nov. pro *A. decumbens.*

Basionym: *A. decumbens* S. Watson

***Atriplex welshii* C. A. Hanson**, Stud. Syst. Bot. Brigham Young Univ. 1: 1. 1962.

= *A. gardneri* var. *welshii* (C. A. Hanson) Welsh

Type: "Utah: Grand Co., 4 mi south of Cisco along state highway 128, July 5, 1961"; C. A. Hanson 322; holotype BRY!; isotypes GH!, ISC!

***Calligonum canescens* Pursh**, Fl. Amer. Sept. 2: 370. 1814.

= *A. canescens* (Pursh) Nuttall

Type locality: Lyman or Buffalo counties, South Dakota, M. Lewis in 1804.

Type: "Big Bend of the Missouri, Sept. 21, 1804," Lewis and Clark Herbarium; lectotype PH!, G. D. Brown, Amer. Midl. Naturalist 55: 209. 1956.

The original description of *Calligonum canescens* Pursh is "C. dioicum, pulverulento-fruticulosum; folis lanceolatis, floribus axillaribus glomeratis in apice ramulorum subspicatis, fructibus alatis, alis venosis cristato-dentatis. In the plains of the Missouri, near the Big bend. H. July, Aug. v.s. in Herb. Lewis. Flowers exceeding small. Goats delight to feed upon this shrub."

The sheet at PH contains three branches, the left one with immature fruit, the middle one sterile, and the one at right with mature fruiting bracteoles. This latter specimen was designated specifically as the lectotype by McNeill et al. (1983); it clearly fits the concept of the species as interpreted by contemporary authors, except for Stutz and Sanderson (1979), who claim that the type belongs to what was subsequently named *A. aptera* A. Nelson, based on the assumption that the Lyman County, South Dakota, type locality is not within the current range of *A. canescens* as presently accepted but is within the range of *A. aptera*. Examination of a great many specimens from throughout the western plains has failed to yield a plant of *A. aptera* with fruiting bracteoles identical to the lectotype, which is matched many times among the specimens traditionally passing as *A. canescens*.

The type sheet bears the designation "Sept. 21, 1804," and the site of the Lewis and Clark camp on that date is adjacent to present Lower Brule, Lyman or Buffalo counties, a short distance above the confluence of the White River. That portion of the Missouri River has been inundated by waters behind the Fort Randall Dam, far downstream. Nuttall had traversed the river corridor in 1811, going upriver as far as Fort Mandan. The description and discussion by Nuttall (1818) of the species is pertinent to the interpretation of the Lewis type material. He describes the plant as about 3 or 4 feet high, with the "calix (i.e., fruiting bracteoles) 2-parted, becoming indurated, acute, with 4 unequal eristated or dentated angles"; the habitat was designated: "On the denudated saline hills of the Missouri [possibly a reference to the lower-growing, variable, *gardneri*-like *A. aptera*]; commencing about 15 miles below the confluence of the White River, and continuing to the mountains [i.e., to the Mandan, as near as he went toward the mountains]." Much of the habitat where plants typical of *A. canescens*, as traditionally interpreted, could have grown is beneath the waters of Fort Randall Dam, and a valid assumption that typical *A. canescens* did not occur there cannot be made. Some plants from areas of South Dakota adjacent to Lower Brule clearly approach typical *A. canescens*. There is no justification for interpretation of the name differently from that used in the historic past.

Obione acanthocarpa **Torrey,** U.S. & Mex. Bound. Bot. 2: 183. 1859.

= *A. acanthocarpa* (Torrey) S. Watson

Type locality: "Plains between the Burro mountains; September, *Bigelow*, (in fruit.) On the Rio Grande, below Presidio del Norte; *Parry*. Near the Piloneilla, Sonora, September"; *Thurber*. (No. 1739; *Wright*. His No. 1737 seems to be a slender form of the same.)

Type: "Rio Grande below Presidio del Norte (El Paso), Aug." Parry s.n.; lectotype NY! (Henrickson Southwest. Nat. 33: 454. 1988); isolectotype NY!

Obione berlandieri **(Moquin-Tandon) Moquin-Tandon,** in de Candolle, Prodr. 13(2): 114. 1849.

Basionym: *A. berlandieri* Moquin-Tandon

= *A. canescens* (Pursh) Nuttall

Obione canescens **(Pursh) Moquin-Tandon,** Chenop. Enum. 74. 1840.

Basionym: *Calligonum canescens* Pursh

= *A. canescens* (Pursh) Nuttall

Obione confertifolia **Torrey & Frémont,** in Frémont, Rep. Explor. Exped. Oregon & California 318. 1845.

= *Atriplex confertifolia* (Torrey & Frémont) S. Watson

Type locality: "On the borders of the Great Salt Lake" (l.c.).

Type: "Obione confertifolia, *Torr. & Frém.* in Frém. 2nd Reprt. (1845). Borders of the Great Salt Lake [near mouth of Weber River, Weber Co.], Utah. 761. 1843"; Frémont s.n. probably 10 September 1843; holotype NY!

This species is noted by Frémont (1845) in his journal entry for 10 September 1843, on his return trip from Disappointment [Frémont] Island. The plant was probably collected on the trip from the water's edge to the camp on the lower Weber River, in Weber Co., Utah. The holotype consists of a single branch in young fruit. The sheet bears the notation in Torrey's handwriting, "Obione rigida var. confertifolia n.sp. (crossed out) T. & F." Below the notation is a drawing of a fruiting bract, with one side folded back, and an ovary. This is clearly the specimen on which the species was based. There is a second sheet at NY!: "Frémont's 2nd Expedn." with the notation "Grayia or near it." The specimen has male inflorescence fragments and clearly is not a portion of the type collection.

Obione coriacea **(Forssk.) Moquin-Tandon,** Chenop. Enum. 71. 1840.

This Egyptian species was compared by Torrey and Frémont (Frémont 1845) with *Obione confertifolia* (see above). It does not occur in North America.

Obione gardneri **Moquin-Tandon,** in de Candolle, Prodr. 13(2): 114. 1849.

= *A. gardneri* (Moquin-Tandon) Dietrich var. *gardneri*

Type locality: SE Wyoming or W Nebraska, "Ad La Platte, Gardn. n. 250" (Moquin-Tandon in de Candolle l.c.).

Type: "Gordon 250. La Platte. Obione Gardneri Moq. A low female plant, lax spike in fruit," possibly 1843; holotype K?; isotype GH!

The fragments at GH consist of a leaf and two immature fruiting bracteoles, probably taken from the type at K (Hooker herbarium), which we have not seen. Writing on the fragment envelope is in ink, but partly illegible. The name of the collector is subject to interpretation, but is presumed to be "Gordon." Moquin-Tandon interpreted it as "Gardner," and named the species after the person assumed by him to be the collector. The epithet was spelled gardneri on purpose and is not an orthographic variant. It is legitimate under stipulations of the International Code.

Obione hymenelytra **Torrey,** in Whipple, Pacif. R. R. Rep. 4: 129. 1857.

= *Atriplex hymenelytra* (Torrey) S. Watson

Type locality: "Hills and gravelly places on the William's River [Bigelow]. This species was found by Dr. Parry and by Colonel Frémont on the Gila" (l.c.).

Type: "Frémont's Expedition to California, 1849. Obione hymenelytra, n. sp." (lectotype NY!, Brown, Amer. Midl. Nat. 55: 203. 1956.). "Frémont's Expedition to California, Gila" [1849] (presumed isolectotypes NY Crooke!, GH!). A third sheet, "Frémont's 2nd Expedition," is at NY! Except for the sheet designated as lectotype, the Frémont materials from 1849 are scanty, consisting mainly of fruiting bracts (presumed isolectotypes NY!, GH!) and a branchlet of equivocal source (GH!). The lectotype at NY bears all of the accoutrements of a Torrey type specimen, except for lack of illustrations, but includes a descriptive label in Torrey's handwriting and the name Obione hymenelytra, n. sp., on the label.

Obione lentiformis **Torrey,** in Sitgreaves Rep. 169. 1854.

= *Atriplex lentiformis* (Torrey) S. Watson

Type locality: California, along the Colorado River, S. W. Woodhouse s.n., 6 November 1851 (Sitgreaves Expedition, November 1851) (l.c.).

Type: "Sitgreaves Report 1851. Obione lentiformis Torr. in Sitgreaves ex Torrey. Rio Colorado, Calif.—Nev. ex Torrey"; "Rio Colorado. Nov. 6th 1851. Dr. Woodhouse"; lectotype NY! (selected by F. V. Coville, Contr. U.S. Natl. Herb. 4: 181. 1894); isolectotype GH!

Obione lentiformis β *rhombifolia* Torrey, Pacific R. R. Rep. 4: 129. 1857.

Type: Arizona, NY?

I have been unable to locate material at NY with this designation nor make a determination as to its disposition taxonomically.

Obione leucophylla **Moquin-Tandon,** in de Candolle, Prodr. 13(2): 109. 1849.

= *Atriplex leucophylla* (Moquin-Tandon) D. Dietrich

Type locality: "In California (Chamisso!), San-Francisco (Barclay!)" (l.c.).

Type: "San Francisco. Barclay"; holotype K!

Obione obovata **(Moquin-Tandon) Ulbrich,** Natur. Pfl. ed. 2. 16(c): 508. 1934.

= *A. obovata* Moquin-Tandon

Obione occidentalis **(Torrey & Frémont) Moquin-Tandon,** in de Candolle, Prodr. 13(2): 112. 1849.

Basionym: *Pterochiton occidentale* Torrey & Frémont

= *A. canescens* (Pursh) Nuttall

***Obione occidentale* var. *angustifolia* Torrey,** in Emory, Bot. Mex. Bound. 2(1): 189. 1848.

= *A. canescens* (Pursh) Nuttall

Type locality: Texas, Valley of the Rio Grande, Wright in 1852.

Type: "Field No. 394. Obione, Sandy ridge on Rio Grande, 3–5 ft tall, much branching, June 17, 1852. Rio Grande below El Paso Texas. [Wright] 1742 = 394"; holotype NY!; isotypes GH! (3 sheets).

All three sheets at GH bear the number 1742 on the label. One of them also has the number 394, which was evidently the field collection number. The number 1742 was subsequently applied. The specimens all have very narrow leaves to ca 4 mm wide and immature fruiting bracteoles. The sheet at GH with the number 394 is doubly mounted with a second Wright collection (1741 = No. 24), which has 4-winged fruiting bracteoles to 7 mm wide. Notes appear above both labels on the sheet. That above 24 reads: "24, Chenop. hills near Frontera, 3–4 ft tall, branching widely, July 19, 1851. *El Paso Co., Texas*"; above 324 is, "324. Obione, sandy ridges on Rio Grande, 3–5 feet tall, much branching, June 17, 1852, *Rio Grande below El Paso, Texas.*" The latter is an isotype. All of the specimens appear to be *A. canescens*, sens. lat.

Specimens with narrow leaves occur here and there throughout the range of the species. Those from western Texas that fit within the concept of var. *angustifolia* seem not to represent a taxon worthy of consideration.

Obione oppositifolia **(S. Watson) Ulbrich,** in Engler & Prantl, Die Natur. Pflanzenf. Ed. 2. 16e: 508. 1934.

Basionym: *Atriplex oppositifolia* S. Watson

Obione polycarpa **Torrey,** in Whipple, Pacific R. R. Rep. 4: 130. 1857.

= *A. polycarpa* (Torrey) S. Watson

Type: Arizona, Graham Co., "With the preceding," i.e., "Hills and gravelly places, on William's River valley of the Gila River [near base of Mt. Graham, ca 13 mi SW of Stafford]," October 28, 1846, Emory s.n.; holotype NY!

Obione rigida **Torrey & Frémont,** in Frémont, Rep. Explor. Exped. Oregon & California 318. 1845 (nom. nud.).

= *Atriplex confertifolia* (Torrey & Frémont) S. Watson

Authentic specimen: "Obione rigida T. & F. On an island [Frémont Island] in Great Salt Lake, [Weber Co., Utah], Frémont 767, 1843"; Frémont s.n., 9 September 1843 (NY!, Torrey!).

The name was published without a description and is a nomen nudum. The specimen was taken on 9 September 1843 when Frémont and his boating party were on Disappointment [Frémont] Island in the Great Salt Lake. It seems clear from the notation that Torrey intended, at least initially, to name the species *O. rigida*, with the specimen taken later on "borders of the Great Salt Lake" as var. *confertifolia* of that species. Reasons for change of mind are not apparent, but Torrey abandoned the epithet *rigida* in favor of *confertifolia*. The application of the same number, in this case 767, to two sheets of the same taxon is in keeping with the practice of Frémont, at least occasionally, of using the number to indicate a species and not a collection. The sheet bears drawings of bracts, fruit, seed, and embryo, roughly sketched by Dr. Torrey.

Obione spinosa **Moquin-Tandon,** in de Candolle, Prodr. 13(2): 108. 1849.

= *A. canescens* (Pursh) Nuttall

Type locality: "In Columbia (Nutt.!). Phyllocarpa spinosa Nutt.! in herb. Hook." (l.c.).

Type: "Lophocarya * *Pterocarya* (crossed out) * *spinosa.* R. Mts of the Columbia. Pt. canescens. Atriplex canescens?," Nuttall s.n.; holotype BM!

This name has consistently been treated as a synonym of *A. confertifolia*, but the Nuttall specimen at BM is *A. canescens.*

Obione tetraptera **Bentham,** Bot. Voyage Sulph. 48. 1844.

= *A. canescens* (Pursh) Nuttall

Type locality: California, San Diego.

Type: "Ex Herbariae Musei Brittanniei Voyage of H.M.S. Sulphur, Capt. F. W. Beechey 1836–37, Capt. E. Belcher, 1837–41. (Type collection of Obione tetraptera Benth.) California, San Diego. Sept–Oct. 1839. Straggling shrub 7–9 ft. Hills San Diego. George W. Barclay 3060"; holotype BM!; isotypes GH!, K!, MO!

The isotypes at GH and K each consist of a large branch with few leaves and fruiting bracteoles still attached. The leaves are up to 4 mm wide and the bracts somewhat laciniate. Specimens approach the "*laciniata*" phase of *A. canescens* and possibly represent intergradation of *A. linearis* with *A. canescens.* The specimen at K bears the label information, "Obione tetrptera. California. Barkley. Hooker 1844."

Obione torreyi **S. Watson,** Rep. Geol. Explor. 40th Parallel 5: 290. 1871.

= *A. torreyi* (S. Watson) S. Watson

Type locality: Nevada, Humboldt Co., dry valleys bordering the Trukee and Carson rivers, Torrey 463 (Watson 1871).

Type: "Herbarium of Columbia College, New York, No. 463. Obione torreyi S. Wats. Sterile saline plains, Humboldt Co., Nevada. Collected by J. Torrey 1865"; lectotype GH! (G. D. Brown, Amer. Midl. Nat. 55: 205. 1956); isolectotype NY!

The holotype at GH is doubly mounted with Parry 280, 1881. It is staminate, with glomerules ca 2 mm thick arranged on short lateral spikes (to ca 1.5 cm long) on lateral branches of a much larger paniculate cluster to 28 cm long. Branches are longitudinally striate and ridged with low, acute ridges.

Phyllocarpa spinosa **Nuttall ex Moquin-Tandon,** in de Candolle, Prodr. 13(2): 108. 1849. pro syn.
= *A. canescens* (Pursh) Nuttall

Pterochiton canescens **(Pursh) Nuttall,** J. Acad. Nat. Sci. Philadelphia 1: 184. 1847.
Basionym: *Calligonum canescens* Pursh
= *A. canescens* (Pursh) Nuttall

Pterochiton occidentale **Torrey & Frémont,** in Frémont, Rep. Explor. Exped. Oregon & California 318. 1845.
A. occidentalis (Torrey & Frémont) Dietrich; *A. canescens* var. *occidentalis* (Torrey & Frémont) Welsh & Stutz
= *Atriplex canescens* (Pursh) Nuttall var. *canescens*

Type locality: "The precise locality of this plant we cannot indicate, as the label was illegible; but it was probably from the borders of the Great Salt lake" (l.c.).

Type: "Pterochiton occidentale Torr. & Frém." Frémont, probably 10 September 1843 [locality data are missing from the type specimen] (holotype NY!; microfiche BRY!).

The herbarium sheet bears a folded sheet of paper with the usual careful and detailed drawings of bracts, embryo, and seed, and the designation "Pterochiton." In the lower right corner of the sheet is written "Frémont, N. Gen. Pterocalyx," and at the bottom center the words "Pterochiton occidentale, Torr. & Frém." The sheet contains three branches, with the bracts mainly fallen away. This sheet was designated as lectoype by G. D. Brown, Amer. Midl. Nat. 55: 209. 1956, but no other specimens are cited with the protologue and the designation should be holotype.

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NEW RECORDS OF SCOLYTIDAE FROM WASHINGTON STATE

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ABSTRACT.—Eighteen species of Scolytidae are reported from Washington state for the first time or raised from obscurity: *Scierus annectens* LeConte, *Hylesinus californicus* (Swaine), *Phloeotribus lecontei* Schedl, *Carphoborus vandykei* Bruck, *Polygraphus rufipennis* (Kirby), *Crypturgus borealis* Swaine, *Pityogenes knechteli* Swaine, *Ips mexicanus* (Hopkins), *Ips perturbatus* (Eichhoff), *Ips plastographus plastographus* (LeConte), *Ips woodi* Thatcher, *Trypodendron betulae* Swaine, *Trypophloeus striatulus* (Mannerheim), *Procryphalus mucronatus* (LeConte), *Procryphalus utahensis* Hopkins, *Pseudopityophthorus pubipennis* (LeConte), *Pityophthorus alpinensis* G. Hopping, and *Pityophthorus grandis* Blackman. Host tree and collection data are given for these species. A total of 105 scolytid species known from Washington are listed.

Key words: Scolytidae, faunal list, Washington state.

Washington is a large state with seven physiographic provinces (Franklin and Dyrness 1973), ranging from sea level (Puget Trough) to over 4450 m on Mount Rainier (southern Washington Cascades). Under the influence of moisture, temperature, and substrate, natural vegetation types range from coniferous forests through woodland to shrubsteppe. Along Washington's western edge, the Coast Range and Olympic Mountains intercept the moisture-laden prevailing winds from the Pacific Ocean, helping to make the temperate forests of western Washington (and northern Oregon) the most dense in the world. They are composed almost exclusively of conifers and in that respect are also unique among temperate forests. Eastward lies the Cascade Range that contains Mount Rainier and other volcanic peaks. Mixed conifers prevail in these mountain ranges. Farther east is the Columbia Basin, largest and most arid of the provinces, occupying virtually the southeast quarter of the state, except for a bulge of the Blue Mountains extending northward from Oregon. Trees of this province are restricted mainly to water courses and urban areas. North of the Columbia Basin is the Okanogan Highlands province, bordering on British Columbia and Idaho, which provides a vegetational bridge to the more diverse northern Rocky Mountain flora.

The provinces of Washington vary greatly in their climate, resulting from complex interplay between maritime and continental air masses and the mountain ranges, particularly the Cascade Range that divides the state into eastern and western parts. For example, Quinalt on the Pacific side of the Coast Range receives 337 cm of precipitation annually, whereas Yakima, in the rain shadow to the east of the Cascade Range, has only 20 cm. Average January and July temperatures for Seattle (Puget Trough) are 4.5°C and 18.7°C, whereas those for Yakima (Columbia Basin) are –2.5°C and 21.7°C.

The Scolytidae of Washington are host specific to varying degrees, and the extent of their diversity is related to the diversity of their woody host plants. Conifers are hosts of 87 species listed herein. A majority of these (81 species) are restricted to one or a few species of Pinaceae in the genera *Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, and *Tsuga*, while six species infest Cupressaceae (*Thuja*, *Chamaecyparis*, and *Juniperus*). The remaining 19 species infest angiosperms (*Populus*, *Salix*, *Alnus*, etc.). By their habits, Washington Scolytidae are characterized as true bark beetles, living in phloem (90 species); ambrosia beetles, living in xylem where they may feed entirely or partly on symbiotic fungi that they transmit (13 species), living in pine cones (*Conophthorus ponderosae* Hopkins), or living in the roots of red clover (*Hylastinus obscurus* [Marsham]).

Patterson and Hatch (1945) listed 73 species of Washington Scolytidae, adjusted to present-day synonymy. Wood (1971, 1982) lists

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Washington in the distribution of 82 species of Scolytidae; six additional species are listed by Wood and Bright (1992). We herein update those publications with 15 new state records collected by us or found in museum collections, and three species collected by M. A. Deyrup (personal communication). Similar lists have been published for Idaho (Furniss and Johnson 1987), Montana (Gast et al. 1989), and Oregon (Furniss et al. 1992).

Additional species of Scolytidae are likely to be collected in Washington in the future. They may include species known to occur in adjacent states or British Columbia, hosts of which occur in contiguous areas of Washington. Also, commerce from foreign countries entering Puget Sound and the Columbia River may bring exotic species accidentally. Species that infest xylem (ambrosia beetles) are especially well adapted to such transport. The establishment of ambrosia beetles, which typically are not very host-specific, is enhanced by the moderate climate and great diversity of native and exotic flora in the Seattle area. Indeed, it is probable that such introduced scolytids may have already gained a foothold there and have not yet been detected.

The following are abbreviations for repositories listed for specimens new to Washington: ABS = Archbold Biological Station, Lake Placid, FL; FS-R1 = Forest Service, USDA, Region 1, Missoula, MT; PNW = Pacific Northwest Forest and Range Experiment Station, Forest Service, USDA, Corvallis, OR; SLW = S. L. Wood, Brigham Young University, Provo, UT; WFBM = W. F. Barr Entomological Museum, University of Idaho, Moscow, ID.

SPECIES NEW TO WASHINGTON

Subfamily Hylesininae

Scierus annectens LeConte

BIOLOGY.—Monogynous. Infests lower bole and roots of felled *Picea* spp., rarely *Pinus contorta*, often by entering a gallery of *Dendroctonus rufipennis* (Kirby). The parent gallery is 3–4 cm long, inclined diagonally across grain. One generation per year (Stewart 1965).

DISTRIBUTION AND NOTES.—CANADA: Alta., B.C., N.B., Newf., Ont., Que., NWT; USA: Alas., Ariz., Calif., Colo., Ida., Me., Mont., N.H., N.M., Ore., Ut.; WASHINGTON: Tieton Ranger Station, Yakima Co., 17-VIII-1955, *Picea engelmannii*, K. H. Wright (4 PNW, 1 WFBM).

Hylesinus californicus (Swaine)

BIOLOGY.—Monogynous. Infests the bole and limbs of *Fraxinus* spp. Egg galleries are transverse and deeply engrave the wood. Overwintering beetles evidently form feeding tunnels in green bark of *Fraxinus* spp. (Wood 1982).

DISTRIBUTION AND NOTES.—MEXICO: Chih.; USA: Ariz., Calif., Colo., N.D., N.M., Okla., Ore. Tex., Ut.; WASHINGTON: Pack Forest, La Grande, Pierce Co., 10-V-1941, *Fraxinus latifolia* (=*oregona*), R. L. Furniss. Two trap trees, 4″ and 7″ diameter, felled 4-III-1941. Pairs of beetles and eggs present in 2.5-cm galleries 10-V-1941. Ten km N Adna, Lewis Co., 14-VII-1991, *Fraxinus latifolia*, M. M. Furniss and J. B. Johnson (approx. 100 WFBM, 2 SLW). Infesting underside of a 12-cm-diameter broken-off branch on ground. Galleries each with a female and male parent, eggs present. Adult progeny reared, some larvae tunneled into xylem for a depth of four annual growth rings before transforming to adults.

Phloeotribus lecontei Schedl

BIOLOGY.—Monogamous. Male constructs an entrance tunnel and the bases of two egg galleries that are then completed by the female. Egg galleries run obliquely across the grain of shaded-out branches in merchantable-size living trees. Adults and larvae may be present throughout the year; overwintering adults may occur in brood galleries, special hibernation or maturation tunnels, or newly formed parental galleries (Wood 1982).

DISTRIBUTION AND NOTES.—CANADA: Alta., B.C.; USA: Ariz., Calif., Colo., Ida., Mont., N.M., Ore., Ut., Wyo.; WASHINGTON: 7 km S Harts Pass, Okanogan Co., 5-VII-1988, *Picea engelmannii*, M. M. Furniss (1 WFBM). Collected from a branch of a 60-cm-diameter windfelled tree. Horseshoe Lake, Skamania Co., 17-VII-1991, *Picea engelmannii*, M. M. Furniss and J. B. Johnson (9 WFBM). New attacks in 1-cm-diameter shaded-out branch, without needles, attached to live tree. Swank Pass, Blewett, Chelan Co., 11-V-1975, *Abies grandis*, M. A. Deyrup (ABS). In a small branch. Same locality and date, *Pseudotsuga menziesii*, M. A. Deyrup (ABS). In a shaded-out branch.

Carphoborus vandykei Bruck

BIOLOGY.—Polygynous, unstudied. Members of the genus infest small, shaded-out branches of living trees or boles of small, suppressed, unthrifty trees. Most species live in host tissue that is drier than is typical for bark beetles (Wood 1982).

DISTRIBUTION AND NOTES.—CANADA: B.C.; USA: Calif., Ore.; WASHINGTON: Heritage Campground, Olympia, Thurston Co., 14-VII-1991, *Pseudotsuga menziesii*, M. M. Furniss and J. B. Johnson (approx. 200 WFBM). Infesting a 2.3-m-long, 6-cm-diameter, broken-off branch with red foliage. Also present was *Pseudohylesinus nebulosus* LeConte. Two to four egg galleries radiated from the central nuptial chamber, deeply etching the sapwood. Egg galleries each extended 2–5 cm, their length inversely dependent upon attack density. Eggs present, laid alternately on opposite sides (not opposite each other) in deep niches at a rate of 6 per cm and sealed with a reddish brown coating of frass. Hatched larvae fed in the phloem, not etching the wood. Some larval mines equaled or exceeded the length of egg galleries but most were shorter and very broad, apparently influenced by brood density. Kept at room temperature, adult brood pulverized the bark and deeply scored the xylem before emerging from very dry branch-wood one and one-half years later. The scored xylem had a powdery white appearance, perhaps due to presence of associated yeast. Carson, Skamania Co., 18-VII-1991, *Pseudotsuga menziesii*, M. M. Furniss and J. B. Johnson (approx. 100 WFBM). Infesting 1–2 1/2-cm-diameter branches of a 25-cm-diameter standing tree that had discolored foliage (dying). Galleries with parent beetles and larvae. Phloem very dry. Little Rock, Thurston Co., 30-IV-1975, *Pseudotsuga menziesii*, M. A. Deyrup (ABS). In a dead branch. Tahuya, Mason Co., 21-VI-1975, *Pseudotsuga menziesii*, M. A. and N. Deyrup (ABS). In a small, suppressed tree.

Polygraphus rufipennis (Kirby)

BIOLOGY.—Polygynous. Recorded commonly from *Picea* spp., especially *P. glauca* and *P. engelmannii*, rarely from other genera of Pinaceae. Occasionally kills small-diameter, suppressed trees, commonly occurs as a secondary species in trunks of felled or dying trees. Two to five egg galleries radiate from each nuptial chamber, most commonly two, each made by a different female. One generation per year (Hilton 1968).

DISTRIBUTION AND NOTES.—CANADA: all provinces; USA: Alas., Ariz., Colo., D.C., Ida., Me., Mass., Mich., Minn., Mont., N.H., N.M., N.Y., N.C., N.D., Ore., Penn., S.D., Tenn., Ut., Ver., W.V., Wisc., Wyo.; WASHINGTON: Evans Creek, King Co.; Nacotta, Pacific Co. (Hilton 1968). Kooskooskie, Walla Walla Co., 28-IX-1955, *Picea engelmannii*, W. J. Buckhorn. Lake Wenatchee, Chelan Co., 22-IX-1955, *Picea engelmannii*, P. W. Orr. Metaline Falls, Pend Oreille Co., 1929–1931, *Picea engelmannii* and *Pseudotsuga menziesii*, H. J. Rust and W. D. Bedard. Parkway, Pierce Co., 17-V-1934, *Pinus contorta*, J. A. Beal. Plain, Chelan Co., 19-IX-1955, *Picea engelmannii*, P. W. Orr. Mt. Rainier N.P., 29-X-1930, *Picea engelmannii*, F. P. Keen and W. J. Buckhorn. Winthrop, Okanogan Co., 22-X-1935, *Picea engelmannii*, R. L. Furniss (all PNW). Horseshoe Lake, Skamania Co., 17-VII-1991, *Picea engelmannii*, M. M. Furniss and J. B. Johnson. Infesting shaded-out branches of a 60-cm-diameter, wind-felled tree (3 WFBM).

COMMENT.—This common beetle is certain to occur throughout the range of *P. engelmannii* in the Cascade Range and Okanogan Highlands. The Pacific Co. record is likely to be in *P. sitchensis*; if so, it is a new host record.

Subfamily Scolytinae

Crypturgus borealis Swaine

BIOLOGY.—Monogamous. This smallest Washington scolytid enters galleries of other bark beetles in stems of conifers (*Abies*, *Picea*, *Pinus*). They then tunnel irregularly into the phloem. Apparently one generation per year, overwintering as adults in the brood galleries (Wood 1982).

DISTRIBUTION AND NOTES.—CANADA: Alta., B.C., Man., N.B., NWT, N.S., Ont., Que., Sask.; USA: Ariz., Colo., Ida., Me., Mich., Mo., Mont., N.M., N.Y., Ore., Penn., S.D., Ut.; WASHINGTON: Harts Pass, Okanogan Co., 5-VII-1988, *Abies lasiocarpa*, M. M. Furniss (6 WFBM). Infesting lower trunk of a 30-cm-diameter standing tree having orangish red foliage and new attacks by *Pityokteines* sp. Seventeen km W Mazama, Okanogan Co., 12-VII-1991, *Abies lasiocarpa*, M. M. Furniss and J. B. Johnson (3 WFBM). Infesting lower trunk of a 25-cm-diameter standing tree having red foliage and abandoned galleries of another scolytid, either *Pityophthorus* sp. or *Pityokteines* sp.

Pityogenes knechteli Swaine

BIOLOGY.—Polygynous. The egg gallery is stellate with 4 to 6 branches radiating from the nuptial chamber. Overwintering stages include larvae, pupae, and adults (Alberta, Canada). One and a partial second generation occur per year at that latitude (Reid 1955).

DISTRIBUTION AND NOTES.—CANADA: Alta., B.C., Sask.; USA: Ariz., Calif., Ida., Mont., Ore., Ut., Wyo.; WASHINGTON: Twisp, Okanogan Co., 12-VIII-1930, *Pinus contorta*, F. P. Keen (2 PNW).

Ips mexicanus (Hopkins)

BIOLOGY.—Polygynous. Not studied. Infests *Pinus* spp.; egg galleries curve outward from a central chamber (Wood 1982).

DISTRIBUTION AND NOTES.—CANADA: Alta., B.C.; MEXICO: Baja Calif., Distrito Federal, Chiapas, Dgo., Hildago, Mex., Mich., Pue., Vera.; GUATEMALA; USA: Alas., Ariz., Calif., Colo., Ida., Mont., Ore., Ut., Wyo.; WASHINGTON: Tieton Ranger Station, Yakima Co., 18-VI-1956, *Pinus albicaulis* (new host record), P. W. Orr (15 PNW, 2 WFBM). Horseshoe Lake, Skamania Co., 17-VII-1991, *Pinus contorta*, M. M. Furniss and J. B. Johnson (3 WFBM). Sparse galleries in 30-cm-diameter standing tree with dead top and mottled (dying) foliage. *Hylurgops porosus* (LeConte) also sparse in base. Umatilla National Forest, 45 km S Pomeroy, Garfield Co., 19-VII-1991, *Pinus contorta*, M. M. Furniss and J. B. Johnson (2 WFBM). Infesting a 23-cm-diameter standing tree with red foliage. Egg gallery deeply etched xylem, its branches aligned more or less with wood grain but curving somewhat and irregular due to several turning niches. Base with moist, sour bark. Also present were *Trypodendron lineatum* (Olivier), *Dendroctonus valens* LeConte, *Orthotomicus caelatus* (Eichhoff), and *Pityophthorus confertus* Swaine. Bremerton, Kitsap Co., 21-IV-1974, *Pinus contorta*, M. A. Deyrup (ABS). In a standing, dead tree.

Ips perturbatus (Eichhoff)

BIOLOGY.—Polygynous. Breeds abundantly in *Picea glauca* logging slash and in tops of trees killed by *Dendroctonus* beetles. Parental galleries have a tuning fork pattern with moderately long larval mines. One generation annually but two sets of egg galleries may be constructed by females in one season (Furniss and Carolin 1977).

DISTRIBUTION AND NOTES.—CANADA: Alta., B.C., Man., N.B., NWT, Ont., Que., Sask., Yukon; USA: Alas., Me., Mich., Minn., Mont.; WASHINGTON: Montesano, Grays Harbor Co., 8-IV-1973, *Picea sitchensis*, M. A. Deyrup (ABS).

Ips plastographus plastographus (LeConte)

BIOLOGY.—Polygynous. Usually infests upper side of fallen *Pinus contorta*, rarely *Pinus ponderosa*. Two or three longitudinal egg galleries radiate from each nuptial chamber. Mature larvae and young adults may bore 1 cm into wood prior to emerging (Wood 1982).

DISTRIBUTION AND NOTES.—CANADA: B.C.; USA: Calif., Ida., Ore., Mont., Wyo.; WASHINGTON: Kettle Falls, Stevens Co., IX-5-1968, Hopkins U.S. no. 54222, *Pinus ponderosa*, F. W. Honing and J. E. Dewey (FS-R1).

Ips woodi Thatcher

BIOLOGY.—Polygynous. Infests large limbs and boles of unthrifty or felled 5-needle *Pinus* spp. Egg galleries parallel, resembling a narrow tuning fork (Wood 1982).

DISTRIBUTION AND NOTES.—CANADA: Alta.; USA: Ariz., Ida., Mont., Nev., N.M., Ut., Wyo.; WASHINGTON: Tieton Ranger Station, Yakima Co., *Pinus albicaulis* (new host), 21-IX-55 to 12-VII-1956, P. W. Orr (26 PNW, 3 WFBM).

Trypodendron betulae Swaine

BIOLOGY.—Monogynous. Tunnels are constructed by females radially through bark into sapwood of *Betula* spp, rarely *Alnus* sp. The main tunnel branches at close intervals, left or right, in the same plane. Eggs are laid in niches oriented above and below the gallery. Larvae excavate short cradles in which they develop and feed on ambrosia fungus. Males are active in keeping the tunnels clean and aerated (Wood 1982).

DISTRIBUTION AND NOTES.—CANADA: Alta., B.C., Man., N.B., N.S., NWT, Ont., Que.; USA: Ida., Me., Mass., Minn., Mont., N.H., N.J., N.Y., S.D., Wisc.; WASHINGTON: Metaline Falls, Pend Oreille Co., 31-V-1930, *Betula occidentalis*, Hopkins no. 19839 (PNW).

Trypophloeus striatulus (Mannerheim)

BIOLOGY.—Monogynous. Unstudied, infests stems of *Salix scouleriana*, *Salix* spp., *Alnus crispa*, and *A. rugosa*.

DISTRIBUTION AND NOTES.—CANADA: Newf., N.S., Que., Yukon; USA: Alas., Colo., Ida., Minn., Ut.; WASHINGTON: King Co., 20-VI-1976, *Populus trichocarpa*, M. A. Deyrup (ABS). In branch.

Procryphalus mucronatus (LeConte)

BIOLOGY.—Monogamous. Infests smooth, outer bark of stems of larger, dying, standing *Populus tremuloides*. Overwinter as larvae and adults; one and one-half to two generations per year (Petty 1977).

DISTRIBUTION AND NOTES.—CANADA: Alta., B.C.; USA: Alas., Colo., Ida., Mont., Nev., N.M., Ore., Ut.; WASHINGTON: Kamiak Butte, Whitman Co., 18-VI-1944, *Populus tremuloides*, M. M. Furniss and Jianlin Zhou (4 WFBM). Infesting a 30-cm-diameter recently dead tree that had no foliage. The bark was necrotic and had an almond odor. New attacks at a density of nine per dm occurred at 10-m-height, 11-cm-diameter. Galleries contained one to two parent beetles, eggs and first instar larvae.

Procryphalus utahensis Hopkins

BIOLOGY.—Monogynous. Unstudied, infests stems of willows, particularly *Salix scouleriana*.

DISTRIBUTION AND NOTES.—CANADA: B.C., Que.; USA: Alas., Calif., Colo., Ida., Ore., S.D., Ut.; WASHINGTON: Bremerton, Kitsap Co., 26-VII-1975, *Salix scouleriana*, M. A. Deyrup (ABS).

Pseudopityophthorus pubipennis (LeConte)

BIOLOGY.—Monogynous. Infests bole and branches of *Quercus* spp. that are felled or recently dead. Galleries aligned horizontally across grain, averaging 5 cm long, closely spaced. Larval mines are mainly hidden in the phloem and oriented longitudinally.

DISTRIBUTION AND NOTES.—CANADA: Southern B.C. (Bright 1976); USA: Calif., Ore.; WASHINGTON: Carson, Skamania Co., 18-VI-1991, *Quercus garrayana*, M. M. Furniss and J. B. Johnson (6 WFBM). Infesting a broken, 20-cm-diameter branch on ground.

Pityophthorus alpinensis G. Hopping

BIOLOGY.—Polygynous. Infests broken branches and twigs of *Larix lyallii*, apparently one generation annually.

DISTRIBUTION AND NOTES.—CANADA: Alta.; USA: Ida., Mont.; WASHINGTON: Harts Pass, Okanogan Co., 11-VII-1991, *Larix lyallii*, M. M. Furniss and J. B. Johnson (3 WFBM). Cadavers collected from old galleries in dead branches 0.5–2.5-cm-diameter. Galleries were branched and variable in shape, each branch containing few (9–11) egg niches; larval mines short, broad, restricted to phloem; adult brood had scored the sapwood as if by feeding.

Pityophthorus grandis Blackman

BIOLOGY.—Polygynous, unstudied. Infests shaded-out branches and young, standing *Pinus ponderosa* (Wood 1982).

DISTRIBUTION AND NOTES.—CANADA: B.C.; USA: Ariz., Calif., Colo., Nebr., N.M., S.D., Tex., Ut.; WASHINGTON: Trout Lake, Klickitat Co., 17-VII-1991, *Pinus ponderosa*, M. M. Furniss and J. B. Johnson (4 WFBM). Infesting 4-cm-diameter standing tree with straw-color foliage. Umatilla National Forest, 53 km S Pomeroy, Garfield Co., 19-VII-1991, *Pinus ponderosa*, M. M. Furniss and J. B. Johnson (1 WFBM). Reared from stem of a small, felled tree.

WASHINGTON SCOLYTIDAE

HYLESININAE

Hylastini

- *Scierus annectens* LeConte
- *Scierus pubescens* Swaine
- *Hylurgops porosus* (LeConte)
- *Hylurgops reticulatus* Wood
- *Hylurgops rugipennis rugipennis* (Mannerheim)
- *Hylurgops subcostulatus subcostulatus* (Mannerheim)
- *Hylastes gracilis* LeConte
- *Hylastes longicollis* Swaine
- *Hylastes macer* LeConte
- *Hylastes nigrinus* (Mannerheim)
- *Hylastes ruber* Swaine

Hylesinini

- *Hylastinus obscurus* (Marsham)
- *Hylesinus californicus* (Swaine)
- *Alniphagus aspericollis* (LeConte)
- *Alniphagus hirsutus* Schedl

Tomicini

- *Pseudohylesinus dispar pullatus* Blackman
- *Pseudohylesinus granulatus* (LeConte)
- *Pseudohylesinus nebulosus nebulosus* (LeConte)
- *Pseudohylesinus nobilis* Swaine
- *Pseudohylesinus pini* Wood
- *Pseudohylesinus sericeus* (Mannerheim)
- *Pseudohylesinus sitchensis* Swaine
- *Pseudohylesinus tsugae* Swaine
- *Xylechinus montanus* Blackman
- *Dendroctonus brevicomis* LeConte

- *Dendroctonus ponderosae* Hopkins
- *Dendroctonus pseudotsugae* Hopkins
- *Dendroctonus rufipennis* (Kirby)
- *Dendroctonus valens* LeConte

Phloeotribini
- *Phloeotribus lecontei* Schedl

Phloeosinini
- *Phloeosinus cupressi* Hopkins
- *Phloeosinus keeni* Blackman
- *Phloeosinus punctatus* LeConte
- *Phloeosinus scopulorum scopulorum* Swaine
- *Phloeosinus sequoiae* Hopkins
- *Phloeosinus serratus* (LeConte)

Hypoborini
- *Chaetophloeus heterodoxus* (Casey)

Polygraphini
- *Carphoborus intermedius* Wood
- *Carphoborus ponderosae* Swaine
- *Carphoborus vandykei* Bruck
- *Polygraphus rufipennis* (Kirby)

SCOLYTINAE

Scolytini
- *Scolytus laricis* Blackman
- *Scolytus monticolae* Swaine
- *Scolytus multistriatus* (Marsham)
- *Scolytus opacus* Blackman
- *Scolytus oregoni* Blackman
- *Scolytus piceae* (Swaine)
- *Scolytus praeceps* LeConte
- *Scolytus rugulosus* (Müller)
- *Scolytus subscaber* LeConte
- *Scolytus tsugae* (Swaine)
- *Scolytus unispinosus* LeConte
- *Scolytus ventralis* LeConte

Micracini
- *Hylocurus hirtellus* (LeConte)

Crypturgini
- *Dolurgus pumilus* (Mannerheim)
- *Crypturgus borealis* Swaine

Dryocoetini
- *Dryocoetes affaber* (Mannerheim)
- *Dryocoetes autographus* (Ratzeburg)
- *Dryocoetes betulae* (Hopkins)
- *Dryocoetes confusus* Swaine

Ipini
- *Pityogenes carinulatus* (LeConte)
- *Pityogenes fossifrons* (LeConte)
- *Pityogenes knechteli* Swaine
- *Pityokteines elegans* Swaine
- *Pityokteines lasiocarpi* (Swaine)
- *Pityokteines minutus* (Swaine)
- *Pityokteines mystacinus* Wood
- *Pityokteines ornatus* (Swaine)
- *Orthotomicus caelatus* (Eichhoff)
- *Ips concinnus* (Mannerheim)
- *Ips emarginatus* (LeConte)
- *Ips integer* (Eichhoff)
- *Ips latidens* (LeConte)
- *Ips mexicanus* (Hopkins)
- *Ips montanus* (Eichhoff)
- *Ips perturbatus* (Eichhoff)
- *Ips pini* (Say)
- *Ips plastographus plastographus* (LeConte)
- *Ips tridens engelmanni* Swaine
- *Ips tridens tridens* (Mannerheim)
- *Ips woodi* Thatcher

Xyloterini
- *Trypodendron betulae* Swaine
- *Trypodendron lineatum* (Olivier)
- *Trypodendron retusum* (LeConte)
- *Trypodendron rufitarsis* (Kirby)

Xyleborini
- *Xyleborus dispar* (Fabricius)
- *Xyleborinus saxeseni* (Ratzeburg)

Cryphalini
- *Trypophloeus salicis* Hopkins
- *Trypophloeus striatulus* (Mannerheim)
- *Procryphalus mucronatus* (LeConte)
- *Procryphalus utahensis* Hopkins
- *Cryphalus pubescens* Hopkins
- *Cryphalus ruficollis* Hopkins

Corthylini
- *Pseudopityophthorus pubipennis* (LeConte)
- *Conophthorus ponderosae* Hopkins
- *Pityophthorus alpinensis* G. Hopping
- *Pityophthorus confertus* Swaine
- *Pityophthorus confinis* LeConte
- *Pityophthorus digestus* (LeConte)
- *Pityophthorus grandis* Blackman
- *Pityophthorus murrayanae* Blackman
- *Pityophthorus nitidulus* (Mannerheim)
- *Pityophthorus pseudotsugae* Swaine
- *Pityophthorus tuberculatus* Eichhoff
- *Gnathotrichus retusus* (LeConte)
- *Gnathotrichus sulcatus* (LeConte)
- *Monarthrum scutellare* (LeConte)

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RELATIVE VULNERABILITY TO EXTIRPATION OF MONTANE BREEDING BIRDS IN THE GREAT BASIN

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ABSTRACT.—Seventy-four species of montane breeding birds were evaluated for their vulnerability to extirpation in the Great Basin. Although none of these species are endemic to the Great Basin, the montane island system results in a unique pattern of species associations. Loss of species from these montane communities could be indicative of region-wide habitat degradation. I ranked susceptibility to extirpation based on seven biological variables: geographic range, population size, reproductive potential, susceptibility to cowbird parasitism, migratory status, and diet specialization. Each variable was weighted equally in its contribution to vulnerability, and scores were the sum of trait scores for each species. Different suites of life-history traits led to similar vulnerabilities. The following 10 montane bird species were categorized as most vulnerable to extirpation from the Great Basin, listed as most to least vulnerable: Olive-sided Flycatcher (*Contopus borealis*), Painted Redstart (*Myioborus pictus*), Hammond's Flycatcher (*Empidonax hammondii*), Veery (*Catharus fuscescens*), Whip-poor-will (*Caprimulgus vociferus*), Lincoln's Sparrow (*Melospiza lincolnii*), Black-backed Woodpecker (*Picoides arcticus*), Three-toed Woodpecker (*P. tridactylus*), Himalayan Snowcock (*Tetraogallus himalayensis*), and Nashville Warbler (*Vermivora ruficapilla*). Species of similar vulnerability scores often were dissimilar in threats related to their vulnerability. No taxonomic patterns in vulnerability were found. This type of analysis should be used proactively to identify vulnerable species or populations and to set priorities for research and management.

Key words: vulnerability, conservation priorities, avian diversity, Great Basin, montane islands.

Extinction of species worldwide is occurring at a high rate (Stanley 1985). For the most part, species disappear following habitat loss (Ehrlich 1988) or after stochastic events eliminate relatively small or isolated populations (MacArthur and Wilson 1967, Shaffer 1981, Gilpin and Soulé 1986, Rabinowitz et al. 1986, Reed 1990). Because time, money, and other resources for species preservation are in short supply, it is imperative to identify the relative susceptibility to extinction, or extirpation, among species to aid in setting conservation and management priorities.

Extremely vulnerable species often are easy to identify because of their scarcity, although sometimes they might be difficult to verify as extant (Solow 1993). Slightly more common species, however, often are difficult to classify by their relative susceptibility to extirpation even if it varies greatly among species (Rabinowitz 1981, Rabinowitz et al. 1986, Reed 1992). Methods that discriminate among species' susceptibility to extirpation would be valuable for setting management priorities. Such methods exist for selecting geographic areas for conservation based on the number or variety of species present (e.g., Kirkpatrick 1983, Margules and Usher 1984, Miller et al. 1987, Scott et al. 1991), but these methods are not applicable to prioritizing conservation efforts among species.

Economic methods can be used to prioritize conservation efforts (Bishop 1978, Hyde 1989), but they do not accommodate nonmonetary appraisals of wildlife conservation goals (Sagoff 1988). The triage method (Myers 1979), whereby species are divided into three categories based on likely success of conservation efforts, might not protect the species that are biologically or anthropocentrically the most important. In the present analysis, I used biological traits to determine the relative susceptibility among species to extirpation.

I analyzed susceptibility to extirpation (local extinction) of bird species breeding in the semi-isolated montane habitats of the Great Basin. This is a classic island-biogeographic system that has been used to test ideas about extinction and colonization processes (e.g., Brown 1971, 1978, Johnson 1975, 1978, Behle 1978, Wilcox et al. 1986, Britton et al. 1994). Although there are no endemic bird species in the Great Basin, loss of species from these montane communities reduces biodiversity and could be indicative of region-wide problems.

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Furthermore, the naturally fragmented habitat of the Great Basin montane forest can act as a model for human-caused fragmentation occurring throughout the world. The 74 species considered here differ greatly in their life histories, abilities to colonize, and susceptibility to extirpation. My goal was to rank species by biological characteristics related to their vulnerability to extirpation, in the anticipation that the information would be useful for setting priorities for research, conservation, and management.

Assessing susceptibility to extirpation involves some type of decision analysis (sensu Maguire et al. 1987). There are many methods available for assessing susceptibility to extirpation, and they vary in complexity from simple classifications to complex multivariate analyses (Table 1). More importantly, classification methods differ in their data requirements. Some systems, such as the IUCN classification scheme (Mace and Lande 1991), are data intensive, while others require far less data (Table 1). The more data available for decision making, the more certain the results, but it is important to chose a method that makes proper use of the available data. Biological data are relatively scarce for birds in the Great Basin. In this analysis, I used a method with intermediate data needs to look at vulnerability to extirpation of 74 montane breeding bird species.

METHODS

I combined the methods of Burke and Humphrey (1987), Millsap et al. (1990), and Rabinowitz et al. (1986) to develop an analysis appropriate for the species and available data. This analysis involved assessment using seven biological characteristics related to persistence ability. Values for each characteristic ranged from 0 to 1, with higher values associated with higher susceptibility to extirpation. Values for each character were summed to arrive at a final score of susceptibility to extirpation from the Great Basin. All variables had the same range so that no single character contributed disproportionately to the susceptibility score (Given and Norton 1993). Himalayan Snowcock and Ruffed Grouse (scientific names are given later) are introduced species in the Great Basin (Alcorn 1988). They were included in the analysis because they are established in the Great Basin avifauna. Variable descriptions used in scoring vulnerability to loss from the Great Basin follow.

GEOGRAPHIC RANGE.—Species distributions were taken from a subset of 20 montane sites from the Great Basin (Johnson 1975). The contribution of this variable to the vulnerability score was calculated as 20 minus the number of ranges on which the species occurs, divided by 20. This results in a value ranging from 0 to 1.0, with higher values associated with fewer ranges occupied by the target species, i.e., greater vulnerability. Mountain ranges here and in Table 2 are numbered the same as in Johnson (1975): 1–Warner, 2–Pine Forest, 3–Santa Rosa, 4–Jarbidge, 5–Raft River, 6–Desatoya, 7–Toiyabe-Shoshone, 8–Ruby, 9–Spruce–S. Pequop, 10–Deep Cr.–Kern, 11–Snake, 12–White-Inyo, 13–Plametto, 14–Grapevine, 15–Panamint, 16–Spring, 17–Sheep, 18–Mt. Irish, 19–Quinn Canyon–Grant, and 20–Highland. Distributional data were supplemented from Behle (1978), Herron et al. (1985), Ryser (1985), Alcorn

TABLE 1. Methods for assessing susceptibility to extirpation and for scoring conservation priorities.

Method	Data intensity	Analysis complexity	Citations
Anthropocentric	low	very low	the history of the world
Decision analysis:			
contingency	low	low	Rabinowitz 1981, Rabinowitz et al. 1986, Kattan 1992, Reed 1992
ordinal	variable	low	Burke and Humphrey 1987, Millsap et al. 1990, this study
classical	variable	medium	Maguire et al. 1987
multivariate	variable	high	Given and Norton 1993
Economic	variable	variable	Bishop 1978, Hyde 1989
Viability analysis	high	high	Kinnaird and O'Brien 1991, Boyce 1992
IUCN	very high	high	Mace and Lande 1991

TABLE 2. Additions to Johnson's (1975) original bird distributions. Site numbers are the same as those used by Johnson (1975) and are listed in Methods. Scientific names are listed in Table 3.

Species	Sites added
American Wigeon	8[A]
Northern Goshawk	3[H], 5[B], 7[H], 10[B], 25[H], 30[B]
Sharp-shinned Hawk	16[H]
Flammulated Owl	3[H], 4[G], 7[H]
Northern Pygmy-owl	16[H]
Short-eared Owl	3[H], 8[H], 16[H], 25[H]
Northern Saw-whet Owl	5[B], 6[H], 11[H], 23[H], 31[H]
Calliope Hummingbird	8[A]
Hammond's Flycatcher	8[A], 10[B]
Olive-sided Flycatcher	5[B], 10[B]
Steller's Jay	5[B]
Red-breasted Nuthatch	3[A], 8[A], 31[A]
White-breasted Nuthatch	5[B]
Golden-crowned Kinglet	8[A]
Ruby-crowned Kinglet	10[B]
Water Pipit	5[B]
Solitary Vireo	5[B]
Orange-crowned Warbler	23[A]
Nashville Warbler	8[A]
Lincoln's Sparrow	5[B], 8[A]
White-crowned Sparrow	10[B]
Himalayan Snowcock	8[A]

[A] Alcorn (1988). [B] Behle (1978). [G] S. Dunham (unpublished data from breeding bird surveys in 1993). [H] Herron et al. (1985)

(1988), and S. Dunham (unpublished data from breeding bird surveys in 1993).

POPULATION SOMEWHERE LARGE?—The other component to the relative rarity of a species is its local abundance. This variable is used regularly in rarity studies and generally is used subjectively, often because detailed numbers are not available (Rabinowitz et al. 1986). Because of this, I use it subjectively as well. The definition of "common" varies by taxa. For example, carnivores typically are less common than insectivores at a given site (Brown and Maurer 1987). Therefore, using a single numeric criterion above which a species is considered "common" will result in a systematic bias in vulnerability scores even if no systematic bias exists in susceptibility to extirpation. Therefore, for a given species, if anywhere in the Great Basin there is a population that is "common" for its taxon, I have given the species a score of 0. Data for this assessment came from Ryser (1985), Alcorn (1988), and breeding bird surveys done during the breeding season by myself or my students.

HABITAT SPECIALIZATION.—Habitat specialists (score value = 1) were defined as species that exist in Nevada only in montane habitat. Limited use outside montane habitat, such as mixed forest or riparian areas, scored .50, and relative generalists were given a value of 0. Data on habitat use came from Ehrlich et al. (1988).

SUSCEPTIBILITY TO COWBIRD PARASITISM.—Although there is extensive literature on the potential effects of Brown-headed Cowbirds (*Molothrus ater*) on passerine reproduction (e.g., Mayfield 1977, Brittingham and Temple 1983), the problem has been little studied in the Great Basin. Brown-headed Cowbirds are seen at high elevations in the Great Basin (Fleischer and Rothstein 1988, Fleischer personal communication), particularly associated with riparian habitat and human impact, including cattle grazing. Also, cowbirds can range far from foraging areas in order to brood parasitize (Rothstein et al. 1984). However, not all species are susceptible to parasitism from cowbirds, and some parasitized species are unaffected (e.g., precocial species). I scored species based on my expectation of potential impact of cowbird parasitism. Only passerines that are open-cup nesters could score above 0; Corvidae received 0. Species known to reject cowbird eggs were given a score of 0. Large hosts that did not eject eggs (larger than a female Brown-headed Cowbird; >39 g; Dunning 1993) were given a value of 0.5. Species that are small and not known to reject eggs were assigned a score of 1. Data came from Friedman (1971), Rothstein (1975), Airola (1986), Marvil and Cruz (1989), and Briskie et al. (1992).

MIGRATORY STATUS.—There is some controversy regarding relative costs of migration versus residency in birds. However, because migrants are dependent on habitats in more than one geographic area, I consider them more vulnerable than nonmigrants. I scored migratory status as no latitudinal migration = 0 (lowest risk), migrates primarily to U.S. = .25, migrates primarily to Middle or South America, winters in nonforest = .50, winters in secondary forest = .75, winters in mature forest = 1.0.

REPRODUCTIVE POTENTIAL.—I considered reproductive potential to be the anticipated ability to recover from a population crash and based it on the first age of reproduction, clutch size, and number of broods within a year (data from Ehrlich et. al. 1988). I classified reproductive potential based on an index. The index was the mean clutch size times the number of broods in a year, divided by the age of first reproduction. With this index, a species that breeds repeatedly, at an early age, and with large clutches will have a low score. When no data were available for number of broods, one brood was assumed. Age at first breeding was assumed to be one for small birds, unless data from the literature indicated otherwise. The relationships between the index, reproductive potential, and risk value were made arbitrarily and are presented in Table 3. Data and references associated with this calculation for each species can be obtained from the author.

DIET SPECIALIZATION.—Information on diet breadth came from Ehrlich et al. (1988), and species were classified as generalists (score = 0), moderate specialists (0.5), or specialists (1.0) based on diet described there. This assessment was subjective, based on number of food types typically in the diet and foraging method used.

With this system, vulnerability scores could range from 0 to 7, with 7 being the greatest probability of extirpation from the Great Basin. One variable not included in the analysis that is important in biological risk to extirpation was local population trends. Local population trends were omitted because they are generally unknown for nongame birds in the Great Basin. Local endemism should be considered in scoring as well, but the Great Basin has no endemic bird species. Another variable that has been suggested as a risk to survival is ground nesting. Traditional thought places ground nesters at higher risk to predation than off-ground nesters (e.g., Ricklefs 1969, Slagsvold 1982, Collias and Collias 1984). However, in a reanalysis of the data, Martin (1993) found that ground nesters were not disproportionately susceptible to depredation. Given this important ambiguity, nest location was omitted from the analysis.

RESULTS AND DISCUSSION

There were 41 additions of various mountain ranges to breeding bird distributions (Table 2). The 74 breeding bird species used in this analysis, their associated scores for each life-history trait, and their vulnerability scores are listed in Table 4. Taxonomy follows the convention of the American Ornithologists' Union (1983). Vulnerability scores ranged from 0.60 for the American Robin (scientific names are found in Table 4) to 5.70 for the Olive-sided Flycatcher and Painted Redstart. None of the variables alone was sufficient to assess vulnerability to extirpation. This has been seen by others (e.g., Burke and Humphrey 1987) and is due to other life-history factors affecting susceptibility to extirpation (Arita et al. 1990). Therefore, range and density estimates alone cannot be used to assess vulnerability to extirpation. Another problem with using range and density as the only criteria for extirpation risk is that slice-in-time assessments of rarity can give misleading results due to natural fluctuations in distribution and population size (Hanski 1985). Species' ranges expand and contract, and population densities can undergo large fluctuations annually, even in long-lived species such as birds. Therefore, being uncommon does not, de facto, make a species vulnerable to extirpation; in contrast, being common does not assure continued presence (e.g., the Passenger Pigeon [*Ectopistes migratorius*]; Bucher 1992).

TABLE 3. Reproductive potential and its relationship to risk score. The index is mean clutch size times the number of broods in a year, divided by the age of first reproduction.

Index value	Reproductive potential	Risk score
<1.5	very low	1.0
1.5–2.9	low	0.75
3–5.9	medium	0.50
6–11.9	medium-high	0.25
>11.9	high	0

Passerines tended to rank as more susceptible to extirpation than other orders, primarily because one threat, vulnerability to cowbird parasitism, did not impact non-passerines. Unlike some earlier studies of birds (Terborgh and Winter 1980, Kattan 1992), I found no taxonomic pattern in susceptibility to extirpation. The 10 species with the highest vulnerability score come from seven families in four orders. There are several likely explanations for this. The first is that no inherent patterns exist. Alternatively, a true taxonomic pattern in extirpation proneness might exist for Great Basin birds but was missed because of incomplete data, because of a subsampling effect (not enough of the Great Basin surveyed), or because the analysis considers only current species (implying that extirpation-prone species are gone).

Many species with similar or identical vulnerability scores were vulnerable for different

TABLE 4. Data used in analyses and vulnerability scorings; variable definitions given in text. Higher values indicate higher susceptibility to extirpation from the Great Basin.

		Criteria						
Species	Vulnerability score	Range	Somewhere large?	Habitat specialization?	Cowbird problem?	Migratory status	Reproductive potential	Diet specialization
Canada Goose (*Branta canadensis*)	1.90	.90	0	0	0	.25	.75	0
Green-winged Teal (*Anas crecca*)	2.90	.90	1	.5	0	.25	.25	0
American Wigeon (*A. americana*)	2.90	.90	1	.5	0	.25	.25	0
Canvasback (*Aythya valisineria*)	2.90	.90	1	.5	0	.25	.25	0
Sharp-shinned Hawk (*Accipiter striatus*)	4.00	.50	1	.5	0	.75	.75	.5
Northern Goshawk (*A. gentilis*)	3.10	.60	1	.5	0	.25	.75	0
Himalayan Snowcock (*Tetraogallus himalayensis*)	4.20	.95	1	1	0	0	.75	.5
Blue Grouse (*Dendragapus obscurus*)	2.75	.50	0	1	0	0	.25	1
Ruffed Grouse (*Bonasa umbellus*)	3.20	.95	1	1	0	0	.25	0
Mountain Quail (*Oreortyx pictus*)	1.90	.65	0	1	0	0	.25	0
Common Snipe (*Gallinago gallinago*)	2.70	.70	1	0	0	.50	.50	0
Flammulated Owl (*Otus flammeolus*)	3.05	.55	0	1	0	.50	.50	.5
Northern Pygmy-owl (*Glaucidium gnoma*)	3.30	.80	1	1	0	0	.50	0
Short-eared Owl (*Asio flammeus*)	2.55	.80	1	0	0	.25	.50	0
Northern Saw-whet Owl (*Aegolius acadicus*)	2.85	.60	0	1	0	.25	.50	.5
Common Nighthawk (*Chordeiles minor*)	2.10	.35	0	0	0	.50	.75	.5
Whip-poor-will (*Caprimulgus vociferus*)	4.70	.95	1	0	0	1	.75	1
Calliope Hummingbird (*Stellula calliope*)	3.15	.65	0	.5	0	.75	.75	.5
Broad-tailed Hummingbird (*Salasphorus platycercus*)	2.30	.05	0	.5	0	.50	.75	.5
Lewis' Woodpecker (*Melanerpes lewis*)	1.90	.90	0	.5	0	.25	.25	0
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	2.55	.30	0	.5	0	.75	.50	.5
Red-breasted Sapsucker (*S. ruber*)	3.15	.85	0	.5	0	.75	.50	.5
Williamson's Sapsucker (*S. thyroideus*)	3.35	.55	0	1	0	.75	.50	.5
Downy Woodpecker (*Picoides pubescens*)	2.10	.60	0	.5	0	0	.50	.5
Hairy Woodpecker (*P. villosus*)	2.00	0	0	.5	0	0	.50	1
White-headed Woodpecker (*P. albolarvatus*)	3.45	.95	1	1	0	0	.50	0
Black-backed Woodpecker (*P. arcticus*)	4.45	.95	1	1	0	0	.50	1
Three-toed Woodpecker (*P. tridactylus*)	4.45	.95	1	1	0	0	.50	1
Olive-sided Flycatcher (*Contopus borealis*)	5.70	.45	1	1	1[a]	.75	.50	1
Hammond's Flycatcher (*Empidonax hammondii*)	5.45	.70	1	1	1[a]	.75	.50	.5
Dusky Flycatcher (*E. oberholseri*)	3.30	.05	0	.5	1	.75	.50	.5
Western Flycatcher (*E. difficilis*)	3.95	.45	0	.5	1	1	.50	.5
Horned Lark (*Eremophila alpestris*)	2.60	.85	0	0	1	.25	.50	0

TABLE 4. Continued.

		Criteria						
Species	Vulnerability score	Range	Somewhere large?	Habitat specialization?	Cowbird problem?	Migratory status	Reproductive potential	Diet specialization
Violet-green Swallow (*Tachycineta thalassina*)	3.00	0	0	1	0	.50	.50	1
Gray Jay (*Perisoreus canadensis*)	2.95	.95	1	.5	0	0	.50	0
Steller's Jay (*Cyanocitta stelleri*)	2.10	.60	0	1	0	0	.50	0
Clark's Nutcracker (*Nucifraga columbiana*)	1.65	.15	0	1	0	0	.50	0
Mountain Chickadee (*Parus gambeli*)	1.50	0	0	1	0	0	0	.5
Red-breasted Nuthatch (*Sitta canadensis*)	2.15	.40	0	.5	0	.25	.50	.5
White-breasted Nuthatch (*S. carolinensis*)	2.10	.10	1	.5	0	0	0	.5
Pygmy Nuthatch (*S. pygmaea*)	1.95	.70	0	.5	0	0	.25	.5
Brown Creeper (*Certhia americana*)	1.65	.40	0	.5	0	.25	.50	0
American Dipper (*Cinclus mexicanus*)	3.25	.50	1	1	0	0	.25	.5
Golden-crowned Kinglet (*Regulus satrapa*)	2.40	.65	0	.5	1	.25	0	0
Ruby-crowned Kinglet (*R. calendula*)	2.65	.15	0	.5	1[a]	.75	.25	0
Western Bluebird (*Sialia mexicana*)	2.55	.80	1	0	0	.25	.50	0
Mountain Bluebird (*S. currucoides*)	1.60	.10	0	.5	0	.25	.25	.5
Townsend's Solitaire (*Myadestes townsendi*)	3.00	.25	0	1	1	.25	.50	0
Veery (*Catharus fuscescens*)	4.90	.90	1	.5	1[a]	.50	.50	.5
Swainson's Thrush (*C. ustulatus*)	3.60	.60	0	.5	1[a]	.50	.50	.5
Hermit Thrush (*C. guttatus*)	2.55	.05	0	.5	1[a]	.75	.25	0
American Robin (*Turdus migratorius*)	0.60	.10	0	0	0	.25	.25	0
Water Pipit (*Anthus spinoletta*)	3.65	.90	0	1	1[a]	.25	.50	0
Solitary Vireo (*Vireo solitarius*)	3.55	.30	0	.5	1	1	.25	.5
Orange-crowned Warbler (*Vermivora celata*)	2.60	.35	0	0	1	.75	.50	0
Nashville Warbler (*V. ruficapilla*)	4.15	.90	0	.5	1[a]	.75	.50	.5
Virginia's Warbler (*V. virginiae*)	3.25	.25	0	.5	1[a]	.75	.25	.5
Yellow-rumped Warbler (*Dendroica coronata*)	2.30	.05	0	.5	1	.50	.25	0
Grace's Warbler (*D. graciae*)	4.05	.80	0	1	1[a]	.50	.25	.5
MacGillivray's Warbler (*Oporornis tolmiei*)	3.35	.35	0	.5	1[a]	.50	.50	.5
Wilson's Warbler (*Wilsonia pusilla*)	3.85	.85	0	.5	1	.50	.50	.5
Painted Redstart (*Myioborus pictus*)	5.70	.95	1	1	1[a]	.75	.50	.5
Western Tanager (*Piranga ludoviciana*)	3.15	.15	0	.5	1[a]	1	.50	0
Green-tailed Towhee (*Pipilo chlorurus*)	1.75	0	0	0	1[a]	.50	.25	0
Fox Sparrow (*Passerella iliaca*)	1.95	.45	0	0	1	.25	.25	0
Lincoln's Sparrow (*Melospiza lincolnii*)	4.60	.85	1	1	1[a]	.50	.25	0

TABLE 4. Continued.

		Criteria						
Species	Vulnerability score	Range	Somewhere large?	Habitat specialization?	Cowbird problem?	Migratory status	Reproductive potential	Diet specialization
White-crowned Sparrow (*Zonotrichia leucophrys*)	2.00	.50	0	0	1	.25	.25	0
Dark-eyed Junco (*Junco hyemalis*)	2.05	.05	0	.5	1	.25	.25	0
Gray-crowned Rosy Finch (*Leucosticte tephrocotis*)	3.70	.95	0	1	1[a]	.25	.50	0
Black Rosy Finch (*L. atrata*)	3.50	.75	0	1	1[a]	.25	.50	0
Cassin's Finch (*Carpodacus cassinii*)	2.50	0	0	1	1[a]	.25	.25	0
Red Crossbill (*Loxia curvirostra*)	3.15	.40	0	.5	1[a]	.25	.50	.5
Pine Siskin (*Carduelis pinus*)	2.40	.40	0	.5	1[a]	.25	.25	0
Evening Grosbeak (*Coccothraustes vespertinus*)	2.35	.85	0	.5	.5[a]	.25	.25	0

[a] Assumed to not eject Brown-headed Cowbird eggs

suites of threats to persistence. That is, some equal scores were made up of low values for one or more characteristic and correspondingly high values for other traits, which balanced in the ranking. This observation is consistent with Rabinowitz's (1981, Rabinowitz et al. 1986) observations of plant species' rarity in Great Britain. It should be noted that this analysis refers to species loss in the Great Basin and does not reflect species-wide vulnerability.

This type of analysis is sensitive to the number of variables included. Adding or deleting characters from the analysis would change scores. For example, if ground nesting were decisively shown to increase vulnerability, it could be added to the analysis and would change relative scores. Results also would be altered if the characteristics were weighted differently. I did not weight any variable as more important than another because of the lack of data that demonstrates the validity of weighting particular traits over others. Arbitrarily assigning different weights in the absence of independent data supporting the weighting would result in unwarranted bias in the vulnerability scores.

The results presented are not absolute rankings for susceptibility to extirpation because data are incomplete and more threats might become apparent, which would have to be added to the analysis. Validity of these results depends entirely on reliability of the data used and how representative the 20 mountain ranges are of the rest of the Great Basin. There is a dearth of distributional and life-history data on many Great Basin birds. Therefore, my results should be taken as a guide for detailed local studies of species and their surrounding communities. Results of these studies can then be used to develop proactive management plans.

Vulnerability Ranks and Management

Vulnerability to extirpation and management priorities are not equal. Scores based strictly on biological variables ignore homocentric values, such as hunting or local traditional uses. For example, the top 10 vulnerable species in this analysis include only one hunted species (an introduced one at that), though others were scored. In addition, how a given rank comes about can affect management priorities. There are four ways a species can have a high score, and they should be interpreted differently for management.

(a) High score occurs when the Great Basin is within the greater bounds of a species' distribution and local declines have reduced a species' range and population sizes in the Great Basin. These species are probably declining because of local problems, and in this analysis might include Mountain Quail and Northern Goshawk. Specific management plans should be enacted to increase population numbers, sizes, and distributions.

(b) High score occurs when the Great Basin is within the greater bounds of a species' distribution, and the species is declining throughout its range. Problems could be occurring on the breeding grounds, wintering grounds, or migratory routes. If the cause of decline is known and can be improved through local management, then this should be done. If the cause of the decline is known, but occurs outside the Great Basin, then I would recommend monitoring populations but not making any management efforts. If the cause of the decline is not known, as for many Neotropical migrants, gather information to determine whether or not local management could improve local or region-wide population conditions. If management efforts are suspected to work, implement them with proper controls and follow-up work. If no effect is found, discontinue management.

(c) High score occurs partly because the Great Basin is at the edge of a species' distribution, thus limiting its local distribution and population sizes. Of the top 10 scored species in this analysis, five have Nevada as part of their distributional boundary. This is possibly the trickiest category for management. Species' ranges fluctuate, and population declines might be range retractions having nothing to do with local conditions. These species should be monitored because range retraction might be an early indicator of a species-wide decline (e.g., Laymon and Halterman 1987). However, it can also indicate local problems that require local management solutions. These species need further investigation.

(d) High score occurs when species has declined severely (thus reducing its range and commonness) but is recovering. Continue existing management efforts, if any, and monitor populations to make sure recovery continues. If it does not, these species belong in one of the other three sub-categories.

In all instances involving management plans, efforts should be made to set up proper studies or experiments to ascertain the limiting factor(s) and the correct method(s) for counteracting the problem (MacNab 1983, Gavin 1989, 1991, Murphy and Noon 1992). This includes monitoring suitable control sites. Without using adequate experimental design, it will not be possible to ascertain the effectiveness of management efforts. Low-score species should still be monitored and management plans developed. Low-score species are those that are closest to recovery or those not threatened and thus have potential for the quickest success from management.

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GRASSHOPPER DENSITIES ON GRAZED AND UNGRAZED RANGELAND UNDER DROUGHT CONDITIONS IN SOUTHERN IDAHO

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ABSTRACT.—Low-density grasshopper populations were sampled at 15 pairs of rangeland sites in south central Idaho. One site of each pair had not been grazed by livestock for at least 10 years. Grazed sites were managed under normal grazing regimes established by the Bureau of Land Management.

Mean grasshopper density was higher on ungrazed sites than on grazed sites. Proportions of *Melanoplus sanguinipes* were higher on ungrazed sites than on grazed sites and were higher on annual grasslands than on other vegetation types. Effects of grazing appeared to be independent of vegetation type.

Proportions of Gomphocerinae, a subfamily of grasshoppers that feeds almost exclusively on grasses, were affected by vegetation type, but not grazing. Crested wheatgrass seedings supported the highest proportions of Gomphocerinae. Proportions of Oedipodinae were affected by grazing and vegetation type. Higher proportions of Oedipodinae were found on grazed sites than on ungrazed sites, and on sagebrush/grass sites than on annual grasslands. Results indicate that livestock grazing during drought conditions tends to reduce grasshopper populations on southern Idaho rangeland.

Key words: Orthoptera, Acrididae, Melanoplus sanguinipes, *livestock grazing, drought, population density, range management.*

Grasshoppers are frequently the most abundant arthropods, in terms of biomass, in the intermountain sagebrush ecoregion of the western United States. As primary consumers they may be important in energy and nutrient cycling, and, at outbreak densities, they compete with livestock and wildlife for forage. Because of their ecologic and economic importance, the potential effects of range management practices on grasshoppers are a concern to those interested in the health of rangeland ecosystems. Several studies have addressed the role of livestock grazing on grasshopper populations (Coyner 1938, Smith 1940, Campbell et al. 1974, Holmes el al. 1979, Capinera and Sechrist 1982, Jepson-Innes and Bock 1989, Quinn and Walgenbach 1990, Miller and Onsager 1991). Onsager (1987) suggested that there is probably geographic variation in grasshopper responses to grazing among rangeland types and their constituent grasshopper communities. To date no studies have investigated the relationship between livestock grazing and grasshopper densities on rangelands in the intermountain region.

This study, conducted during years of below-normal precipitation and low grasshopper densities, examined differences in grasshopper densities between rangeland under normal livestock grazing regimes administered by the Bureau of Land Management and rangeland that had not been grazed for at least 10 years.

STUDY AREA

The study area is located southeast of Shoshone, ID, within the Bureau of Land Management's (BLM) Shoshone District, between longitude 114°30′ and 114°00′ W and latitude 42°37.5′ and 43°00′ N. This area receives an average of about 26 cm of precipitation annually, most of it between October and May. Average annual temperature is about 9.0°C.

The intermountain sagebrush ecoregion was subjected to heavy grazing pressure in the late 19th and early 20th centuries, frequent fires, and subsequent invasion by cheatgrass and other exotic plant species (Pickford 1932, Stewart and Hull 1949, Mack 1981, Yensen 1982). As a result, stands of grazing-intolerant native grasses were greatly diminished over much of the region, and cheatgrass has become the dominant species on more than 40 million ha of the Intermountain West (Mack 1981, Pellant and Hall 1994). The present vegetation within the study area consists primarily of cheatgrass, *Bromus tectorum* L., with sagebrush, *Artemisia tridentata wyomingensis* Beetle &

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Young and *A. tridentata tridentata* (Rydb.) Beetle, where it has not burned recently. As of 1988, about 23% (ca 40,000 ha) of the study area consisted of crested wheatgrass, *Agropyron cristatum* (L.) Gaertn., plantings (USDI-BLM 1984, 1990).

MATERIALS AND METHODS

Ungrazed sites were selected on the basis of grazing history (not grazed for at least 10 years), size (at least 16 ha), and shape (at least 100 m across the narrowest dimension). Fifteen rangeland sites were found within the study area that met these criteria. Most sites were isolated tracts fenced to exclude livestock and to provide habitat for upland game birds. Grazing by wildlife within the ungrazed tracts was negligible. Black-tailed jackrabbits were not abundant during the years in which sampling took place, and populations of pronghorn antelope, the only other large vertebrate herbivore present in the summer, are quite low and widely dispersed across the study area, ca 300 individuals over 180,000 ha (J. Russell, USDI-BLM, personal communication).

A grazed site was selected to match each ungrazed site for a total of 30 sites. In most cases grazed sites were adjacent to, and shared a boundary with, ungrazed sites. For six sites adjacent matched pairs were not possible; consequently, grazed sites were chosen within 2 km. All grazed sites matched the ungrazed sites in soil type, topography, vegetation, slope, and aspect. All grazed sites were located within BLM-administered grazing allotments. Stocking rates for the grazed sites varied from 1.9 to 2.8 ha/AUM (USDI-BLM 1990). Not all grazed sites were grazed each year, as prescribed by rest-rotation grazing management plans.

Elevation of the sites ranged from 1180 to 1320 m. Five pairs of sites were located on areas replanted with crested wheatgrass, four pairs were on annual grassland sites having little or no sagebrush, and six pairs were located on sagebrush-grass sites.

GRASSHOPPER AND VEGETATION SAMPLING.—Grasshoppers were sampled on 19 July–7 August 1990 (adult stage), 21–28 June 1991 (primarily nymphal stage), and 2–13 August 1991 (adult stage). Corresponding sites of a grazed and ungrazed pair were always sampled on the same day. Grasshopper density on a site was estimated by counting the number of grasshoppers flushed from 50, 0.1-m^2 rings 5 m apart in a circular transect (Richards and Waloff 1954, Onsager and Henry 1977). Species composition on a site was determined by a "flush-capture" method (Capinera and Sechrist 1982). Thirty to 100 specimens were captured and identified at each site on each sampling date by slowly walking in a circular transect and, to avoid bias toward more conspicuous species, counting only those grasshoppers encountered directly in the path of the observer.

Vegetation was sampled on the same dates as the grasshopppers by visually estimating the percentage ground cover in 5% increments by plant species in each of 40, 0.1-m^2 square quadrats in a circular transect. Plant species unidentifiable in the field were collected and identified later. The percent cover of cryptogams, cattle dung, and bare ground was also estimated. Vegetation data from the three sampling dates were combined for subsequent analyses.

DATA ANALYSIS.—We classified the sites into three vegetation types based on dominant vegetation on a site. Sites that had been seeded to crested wheatgrass were categorized as replanted. Sites with sagebrush as the dominant plant species were placed in the sagebrush category, and the remaining sites, dominated by cheatgrass without significant sagebrush cover, were categorized as annual grasslands.

Differences in percentage ground cover among vegetation types were confirmed with a Kruskal-Wallis non-parametric one-way analysis of variance (Zar 1984). Non-parametric statistical tests were used with the ground cover data because of the large number of zero values involved. Comparisons between vegetation types were made with a non-parametric analog of Tukey's test (Dunn 1964, Zar 1984).

Because paired sites were in close proximity and of similar vegetation, we used Wilcoxon paired-sample tests to identify differences in percentage ground cover between grazed and ungrazed sites.

Grasshopper densities were too low to conduct meaningful statistical comparisons separately for all species. Accordingly, analyses were conducted on densities of total grasshoppers, on proportions of *Melanoplus sanguinipes* (the major pest species in the region), and on proportions of the three subfamilies of Acrididae within the region, Melanoplinae, Gomphocerinae, and

Oedipodinae. Grasshopper densities were transformed by $\log_e(x + 1)$ to normalize the data. The arcsin transformation was applied to the proportions (Zar 1984).

Three-way analysis of variance (PROC GLM, SAS Inst.) was used to determine the significance of sampling date, vegetation type, and grazing treatment effects on grasshopper density and proportions. For the ANOVA, sites were not blocked by location; i.e., pairing was ignored. Comparisons among vegetation types were made with least significant difference mean separation tests (PROC GLM, SAS Inst.). Paired-sample *t* tests were used for comparisons between grazing treatments.

Trends between habitat characteristics and grasshopper densities/proportions were evaluated by Spearman rank correlations (PROC CORR, SAS Inst.). Mean values from the three sampling dates were used for the correlation analyses.

RESULTS

The replanted vegetation type was dominated by crested wheatgrass and also had the greatest amount of bare ground (Table 1). Annual grasslands were dominated by annual plant species, primarily cheatgrass (Table 1). Sagebrush sites had the greatest shrub cover, although other vegetation types had small amounts of sagebrush (Table 1). Annual grasslands and sagebrush sites had little perennial grass cover, other than *Poa sandbergii*.

Grazing treatment did not greatly affect most ground cover variables (Table 2), but sites grazed by livestock had more bare ground and cattle dung and less total vegetative cover and perennial grass cover than the permanently ungrazed sites.

Twenty-three species of grasshoppers were indentified from the 30 sites. *Melanoplus sanguinipes* was found at all 30 sites and represented 36% of all grasshoppers on the study sites. Other common species included *Oedaleonotus enigma* (Scudder), *Ageneotettix deorum* (Scudder), *Aulocara elliotti* (Thomas), *Conozoa sulcifrons* (Scudder), and *Trachyrachys kiowa* (Thomas). No species other than *M. sanguinipes* comprised more than 10% of all grasshoppers from all sites. Total density of grasshoppers on the three sampling dates ranged from <0.2 to 2.6 per m^2.

TABLE 1. Median (s.d.) percentage ground cover by vegetation type.

Ground cover variables	Vegetation type Replanted (*N* = 10)	 Sagebrush (*N* = 12)	 Annual grasslands (*N* = 8)
Annual grasses	1.2b[1] (3.7)	7.8b (8.1)	20.0a (9.0)
Annual forbs	0.5a (1.6)	1.2b (3.9)	3.1b (2.8)
Agropyron cristatum	16.8a (7.2)	0.0b (0.02)	0.0b (0.03)
Poa sandbergii	6.9a (4.9)	5.0a (1.7)	12.0a (5.4)
Other perennial grasses	0.1a (0.4)	0.6a (2.9)	1.1a (2.8)
Sagebrush	0.0b (2.8)	13.0a (5.0)	0.0b (2.4)
Total vegetation	26.1a (8.6)	32.9a (5.7)	41.8b (8.9)
Cryptogams	1.8a (3.2)	7.0b (5.9)	3.1ab (4.3)
Bare ground	40.5a (13.7)	24.0ab (6.5)	18.0b (8.3)

[1] Measures within rows followed by different letters are significantly different, $P < .05$, non-parametric analog of Tukey's test (Dunn 1964, Zar 1984).

Total density of grasshoppers was affected by sampling date and grazing treatment (Table 3). No differences in density were detected among vegetation types (LSD mean separation, $P = .05$; Table 3, Fig. 1).

Proportions of *M. sanguinipes* and all species within the subfamily Melanoplinae were affected by sampling date, vegetation type, and grazing treatment (Table 3). Annual grasslands had the highest proportions of *M. sanguinipes* and of all species within the subfamily Melanoplinae (LSD mean separation, $P = .05$; Fig. 1). The proportion of grasshoppers within the subfamily Gomphocerinae was strongly affected by sampling date and vegetation type, but not grazing (Table 3). Replanted (crested wheatgrass) sites had the highest proportions of Gomphocerinae (LSD mean separation, $P = .05$; Fig. 1). Proportions of grasshoppers within the subfamily Oedipodinae were significantly affected by sampling date, vegetation type, and grazing, although F-values were not as great as for proportions of the other subfamilies (Table 3). The mean proportion of

TABLE 2. Comparison of median (s.d.) ground cover between grazed and ungrazed sites.

	Grazing treatment	
	Grazed	Ungrazed
Annual grasses	10.0 (8.5)	7.0 (12.3)
Annual forbs	1.0 (1.9)	1.5 (3.8)
All perennial grasses*	3.0 (6.4)	4.3 (11.3)
Poa sandbergii	8.7 (5.6)	7.1 (4.9)
Sagebrush	3.0 (7.1)	3.0 (6.8)
Total vegetation*	32.5 (7.6)	39.9 (6.3)
Cattle dung[1]	0.7 (0.5)	0.0 (0.0)
Cryptogams	4.6 (5.7)	6.2 (6.3)
Bare ground**	31.0 (13.4)	23.0 (10.2)

[1] Because no cattle dung was recorded on the ungrazed sites, no statistical test of significance was performed.

*Measures are significantly different ($P < .05$, Wilcoxon paired-sample test, $N = 15$).

**Measures are significantly different ($P < .01$, Wilcoxon paired-sample test, $N = 15$).

Oedipodinae was greater on sagebrush sites than on annual grassland sites (LSD mean separation, $P = .05$; Fig. 1).

The effect of grazing treatment was consistent across vegetation types and sampling dates for all grasshopper variables (Table 3). Because no significant interactions between date and grazing, or vegetation type and grazing, were detected (Table 3), comparisons of grazing treatments were made across all vegetation types and sampling dates.

Overall density of grasshoppers was greater on ungrazed than on grazed plots (paired-sample t test, $P < .001$; Fig. 2). Proportions of *M. sanguinipes* and of all species of Melanoplinae combined were higher on the ungrazed sites (paired-sample t test, $P < .005$; Fig. 2). Oedipodinae showed a trend opposite that of the Melanoplinae, being found in greater proportions on the grazed sites (paired-sample t test, $P < .001$; Fig. 2). Proportions of Gomphocerinae were not affected by grazing (paired-sample t test, $P > 0.10$; Fig. 2).

Total grasshopper density was not correlated with any ground cover variables. Proportion of *M. sanguinipes* was negatively correlated with percentage bare ground and cover of perennial grasses ($r_s = -.59$ and $-.62$, respectively, $N = 30$, $P < .001$), and was positively correlated with percentage ground cover of cheatgrass and annual forbs ($r_s = .41$ and $.42$, respectively, $N = 30$, $P < .05$). Proportion of all Melanoplinae combined was correlated positively with cheatgrass ($r_s = .52$, $N = 30$, $P < .01$) and negatively with perennial grasses and percentage bare ground ($-.70$ and $-.64$, respectively, $N = 30$, $P < .001$).

As proportions of Melanoplinae declined with increasing cover of perennial grasses and bare ground, proportions of other species increased. Gomphocerinae showed trends opposite those of the Melanoplinae. Proportions of Gomphocerinae were correlated positively with perennial grasses and bare ground (.66 and .46, respectively, $N = 30$, $P < .01$) and negatively with cheatgrass and annual forbs ($-.52$ and $-.42$, respectively, $N = 30$, $P < .05$). Proportions of Oedipodinae were not significantly correlated ($P > .05$) with any of the ground cover variables.

DISCUSSION

Grazing influenced both total density and species composition of grasshoppers. Members of the subfamily Melanoplinae accounted for most of the increase in total density on ungrazed sites. Although vegetation did not affect density in this study, it strongly influenced species composition. Relative abundance of Gomphocerinae increased, and Melanoplinae decreased, with increasing coverage of perennial grasses and bare ground, while total numbers of grasshoppers remained the same. Proportions of *M. sanguinipes*, the primary pest species in the region, were negatively associated with grazing, perennial grasses (primarily crested wheatgrass), and percentage bare ground.

Habitat preferences of *M. sanguinipes*, or any organism, represent an integrated response to many stimuli. Short-term changes in habitat due to grazing may include reduced quantities of food, less escape space, increased amounts of bare ground, altered host plant quality, and changes in microhabitat temperature and

TABLE 3. Summary of Type III F-values (and significance levels) from three-way ANOVA for densities of total grasshoppers, *Melanoplus sanguinipes*, Melanoplinae other than *M. sanguinipes*, Gomphocerinae, and Oedipodinae.

Source	d.f.	Grasshopper density/m^2	Percentage *Melanoplus sanguinipes*	Percentage Melanoplinae	Percentage Gomphocerinae	Percentage Oedipodinae
Date (D)	2	12.9 (<.01)	18.7 (<.01)	11.9 (<.01)	21.3 (.01)	6.1 (<.01)
Vegetation type (V)	2	1.2 (.30)	19.3 (<.01)	29.3 (<.01)	22.2 (<.01)	5.6 (<.01)
Grazing (G)	1	5.6 (.02)	13.4 (<.01)	11.7 (<.01)	0.5 (.50)	8.8 (<.01)
V × D	4	2.1 (.09)	2.2 (.07)	2.8 (.03)	1.9 (.13)	1.2 (.34)
G × D	2	0.6 (.58)	0.3 (.77)	0.1 (.88)	2.1 (.13)	0.7 (.48)
V × G	2	0.7 (.49)	0.1 (.89)	0.1 (.87)	0.8 (.43)	0.9 (.43)
D × V × G	4	0.3 (.91)	0.6 (.69)	0.5 (.76)	0.2 (.96)	0.2 (.93)

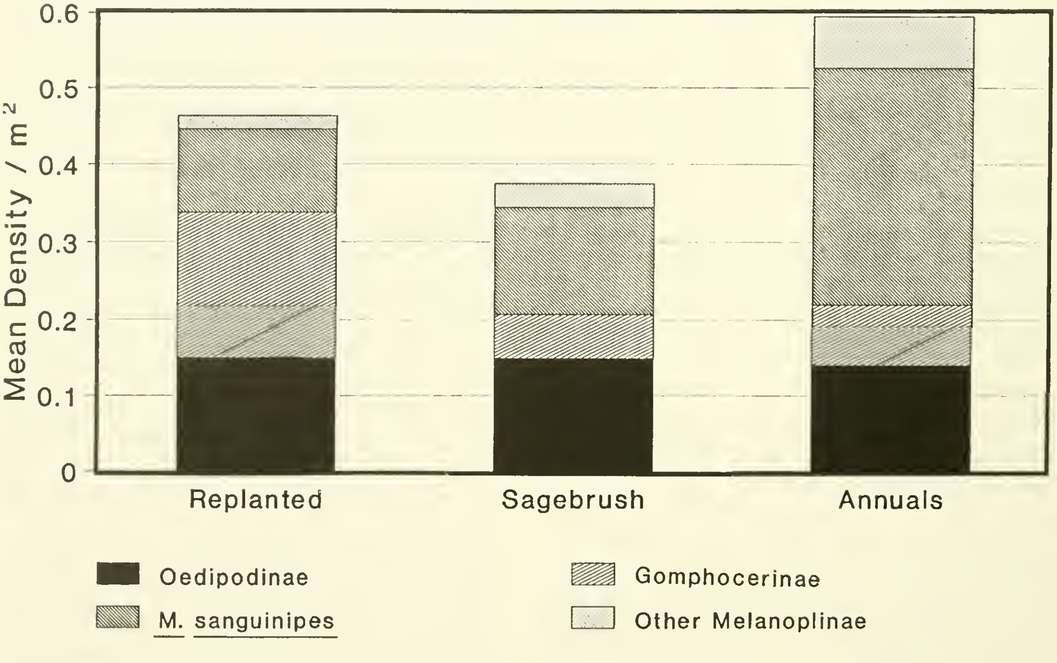

Fig. 1. Mean density of Oedipodinae, Gomphocerinae, Melanoplinae other than *Melanoplus sanguinipes*, and *M. sanguinipes* by vegetation type.

humidity. Differences in plant species composition between grazing treatments were minimal, indicating that long-term alteration of the plant community composition was probably not a factor.

Results of this study are consistent with some previous studies. Proportions of *M. sanguinipes* were negatively correlated with crested wheatgrass in this study. Fielding and Brusven (1992) demonstrated that crested wheatgrass is not a preferred host plant for *M. sanguinipes* in southern Idaho. Perennial grasses are favored food plants for *Aulocara elliotti* (Pfadt 1949, Fielding and Brusven 1992), the most common gomphocerine in the study area. Proportions of *M. sanguinipes* were also negatively correlated with percentage bare ground. Nerney and Hamilton (1969) and Kemp and Sanchez (1987) reported that *M. sanguinipes* avoids oviposition in bare soil, whereas *A. elliotti* prefers to oviposit in bare ground (Kemp and Sanchez 1987, Fisher 1992). High percentages of bare

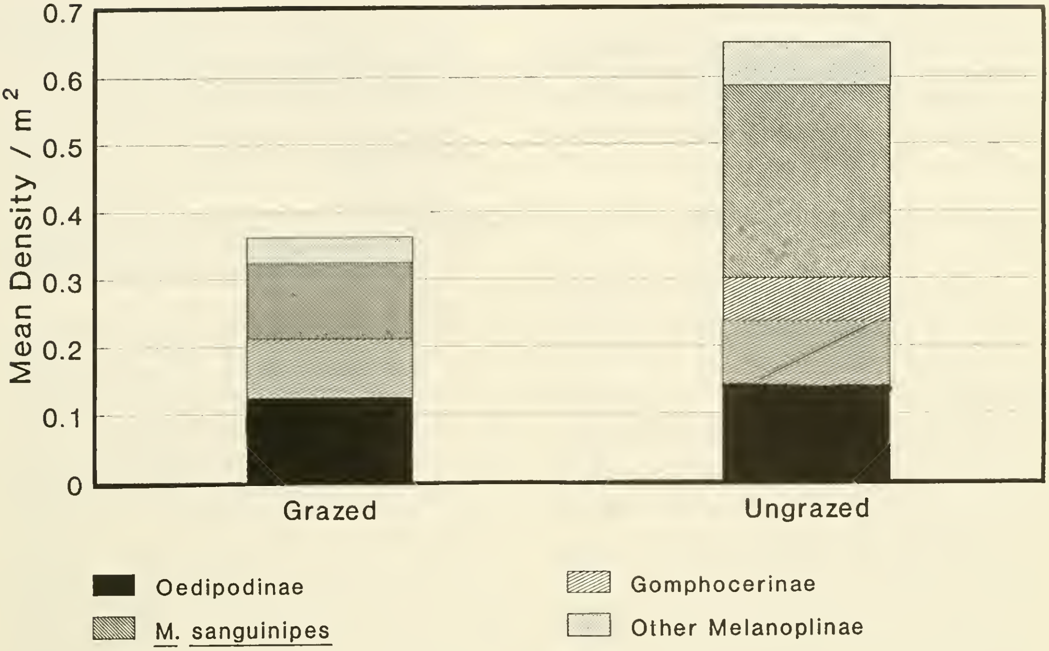

Fig. 2. Mean density of Oedipodinae, Gomphocerinae, Melanoplinae other than *Melanoplus sanguinipes*, and *M. sanguinipes* by grazing history.

ground were associated with both grazing and crested wheatgrass seedings in the present study (Tables 1, 2).

Previous studies that examined grazing effects on grasshoppers reported results similar in some respects to those reported here. On the short-grass prairie of Colorado, Capinera and Sechrist (1982) reported that Oedipodinae were most abundant on the most heavily grazed pastures, while lightly grazed pastures supported the highest total grasshopper densities. Quinn and Walgenbach (1990) found Melanoplinae, particularly *Melanoplus sanguinipes,* to be dominant on ungrazed sites on mixed-grass prairies of South Dakota, even though total grasshopper abundance was less than on grazed sites. However, Miller and Onsager (1991) were unable to detect any effect of different grazing regimes on adult grasshopper populations, including *M. sanguinipes*, in a crested wheatgrass pasture in Montana.

Our observations were made under conditions of low grasshopper density and drought in southern Idaho. Fielding and Brusven (1990) showed that grasshopper population density in southern Idaho was positively correlated with precipitation. Results of this study cannot be extrapolated to predict how grasshopper populations will respond to livestock grazing during more favorable years when rangeland productivity is high and grasshopper populations are rapidly expanding.

Rangeland grasshoppers have traditionally been viewed solely as destructive rangeland pests. However, in an ecosystem context they may have net beneficial worth during most years as an important food source for at least a part of the life cycle of many species of mammals, birds, and reptiles. Results presented here may serve as a cautionary note regarding rangeland ecosystem management under drought conditions. Grazing during years of drought and low grasshopper populations could conceivably add to the stress experienced by insectivorous animals by reducing available food resources (i.e., grasshopper populations), especially if other arthropods serving as alternate foods are also at low densities.

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PLANT NOVELTIES IN *LEPIDIUM* (CRUCIFERAE) AND *ARTEMISIA* (COMPOSITAE) FROM THE UINTA BASIN, UTAH

Stanley L. Welsh[1] and Sherel Goodrich[2]

ABSTRACT.—Named as new taxa are *Lepidium huberi* Welsh & Goodrich, sp. nov., and *Artemisia nova* A. Nels. var. *duchesnicola* Welsh & Goodrich, var. nov. The taxa are provided with diagnoses and descriptions, and their relationships, provenance, and habitats are discussed.

Key words: Lepidium huberi, Artemisia nova *var.* duchesnicola, *new taxa, Utah, Uinta Basin.*

Noted historic pioneer Utah botanist Marcus Eugene Jones (1852–1934) has been quoted, perhaps apocryphally, as saying that he felt sorry for all future generations of botanists because so few plants remained for them to describe and name. Whether the quote is true or not, the generations beyond Jones' time have not suffered from a shortage of areas of botanical inquiry, including the discovery and naming of scores of plants new to science, and there are indications that future generations of botanists beyond the 1990s will continue to find and describe novelties. The flora is not yet fully understood.

The Uinta Basin harbors numerous narrow endemics in many genera of plants, due in some part to the availability of unique geological substrates. Geomorphological processes have, through time, exposed geological strata of varying and diverse composition around the periphery of the basin and onto the slopes of mountains and plateaus that form its borders. The basin proper is the result of uplift during and following the Laramide Revolution, which resulted in a topographically low area south of the Uinta Mountains and north of the Tavaputs Plateau. The exposed strata vary in age from the present into the remote Precambrian epoch. Revealed are mud and siltstones, shales, sandstones, limestones, and quartzites of enormous total thickness, each displayed in sequence like pages from a book. Some of the strata, especially the shales and mud and siltstones, weather into fine-textured, salt-laden substrates, others into sand and gravel, and still others into platy shales. Each of the substrates presents a different array of texture, salinity, trace elements, and other features important to plant growth. Plants have become adapted to the peculiarities of salt content or its lack, to textural differences, and to the peculiarities of water relationships. During the past several millions of years formations have been exposed and cut by erosional processes, and during that same period floras have developed. Varying attributes of the resulting erosional surfaces have allowed the evolution of present floras of the basin. Some Uinta Basin plant endemics are directly correlated to geological formations and are aligned along the strike of formations as though planted mechanically by some gigantic drill. In others the correlation is more subtle, but most endemics show some affinity to particular formations.

The present paper deals with two more narrowly restricted Uinta Basin endemics. Both of them have been known in collections since the 1980s.

Lepidium huberi
Welsh & Goodrich, sp. nov.

Similis *Lepidio montano* var. *alyssioides* in habitu generali amplitudine sed foliis praecipue caulinis (foliis basalibus nullis vel evolutis debiliter) in basim lignosam et in siliculam amplitudinam differt.

Plants subshrubs, the stems woody at the base, ashy or brownish, 1–2.5 dm long; branches puberulent throughout, green, 15–53 cm long; leaves all cauline, the eophylls reduced, principal lower leaves 2–3.5 cm long, 8–20 mm wide, pinnatifid, 5- to 7-lobed, the lobes often again lobed or dentate, smaller and entire upwards; panicles 3–10 (14) cm long, branches corymbosely arranged; pedicels 2–4.5 mm long, puberulent; sepals glabrous, 1.4–1.9 mm long, oval, green, the margin white; petals white, 2.3–2.6 mm long, 1.8–2.2 mm wide, shallowly incised, the style 0.4–0.8 mm long (Fig. 1).

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Suffrutices, caules lignei ad basin, cinerei vel brunneis, 1–2.5 dm long; rami puberulenti omnino, virides, 15–53 cm longi; folia totus caulina, cophyllis reductis, principalibus infernis foliis 2–3.5 cm longis et 8–20 mm latis, pinnatifidis, 5- to 7-lobatis, lobi plerumque lobati vel dentati, parvascens et integra sursum; paniculae 3–10 (14) cm longae, ramis corymbose dispositis; pedicelli 2–4.5 mm longi, puberulenti; sepala glabra, 1.4–1.9 mm longa, ovales, virides, marginibus latis albis; petala alba 2.3–2.6 mm long, unquibus 1 mm longis; staminalis filamenti glabra; siliculae glabrae, ovatae vel ovales, ca 2.3–2.6 mm longae, 1.8–2.2 mm latae, incisura vadosa, styli 0.4–0.8 mm longi.

TYPE:—USA: Utah: Uintah County, growing under ledges of Park City (Phosphoria) Formation, above Weber Sandstone, T2S, R21E, S15 NE1/4, Big Brush Creek Gorge, Uinta Mountains, adjacent to black sagebrush/grass community, west exposure, at 2179 m elev., A. Huber 2400, 18 August 1994 (Holotype BRY; isotypes to be distributed). Additional collections: USA: Utah: Uintah County, 8 km N of Maeser, at base of Taylor Mountain, S. Goodrich, 1548, 13 August 1973; do, T1S, R20E, S30, Ashley Creek, drainage N of Sims Peak, 30 km N of Vernal, at 2959 m, D. Atwood 9128a, 30 July 1982; do, T2S, R21E, S34, SW/SW, N side of Red Mts., ca 16 km N of Vernal, at ca 2320 m, J. Tuhy 2693, 31 July 1986; T2S, R21E, S14 NW/SW, Big Brush Creek Gorge, A. Huber 858, 13 June 1994; do, A. Huber 880, 14 June 1994; do, T3S, R21E, S34, SW/SW, N slope of Red Mountain, ca 6.5 km NW of Steinaker Reservoir, A. Huber & S. Goodrich 2390, 18 Aug. 1994; do, T3S, R21E, S3 NE1/4, Red Mt., ca 6 km NW of Steinaker Reservoir, A. Huber & S. Goodrich, 2392, 18 Aug. 1994; do, T2S, R21E, S34 SW/SE, Red Mt., ca 6 km NW of Steinaker Reservoir, A. Huber & S. Goodrich 2393, 18 August 1994 (all BRY, with numerous duplicates to be distributed).

There is a collection, apparently of this, taken from Moffat County, CO (R. C. & K. W. Rollins 8387, off county roads 13 and 789, S of Hamilton), at BRY. Its main difference is the merely toothed unlobed leaves. Pinnately lobed leaves are featured prominently in the material from the range of the species in Uintah County.

The following key will serve to distinguish *L. huberi* from other members of the *L. montanum* complex.

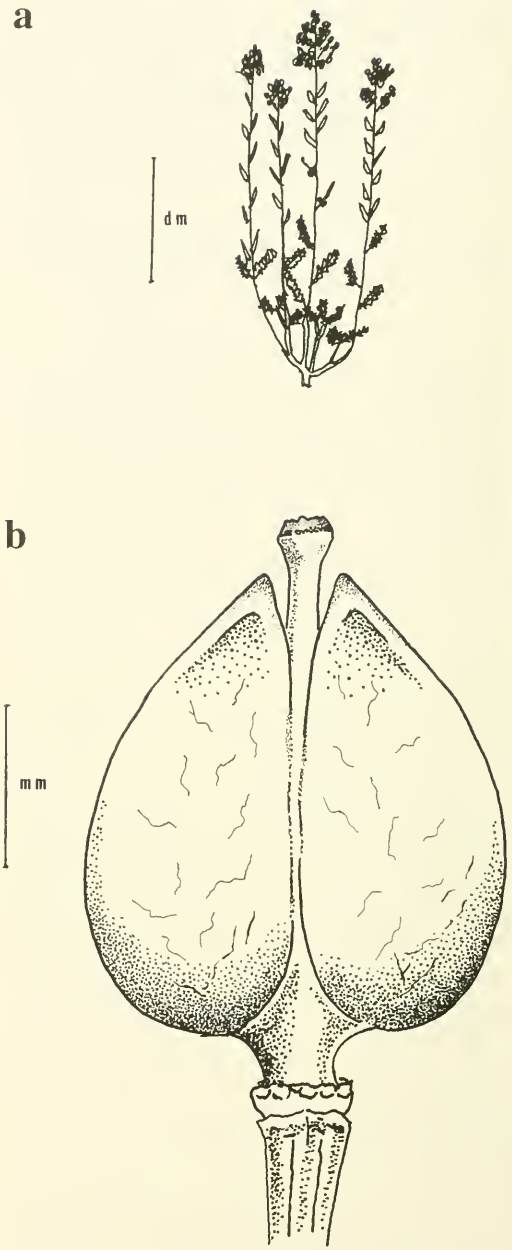

Fig. 1. Habit sketch (a) and silicle (b) of *Lepidium huberi* Welsh & Goodrich.

1. Plants slightly if at all woody above the base, biennial to perennial herbs; silicles 2.8–4.1 mm long, 2.1–2.5 mm wide . . . . *L. montanum* sens. lat.

— Plants woody well above the base, long-lived perennial subshrubs; silicles various 2

2(1). Silicles 4.5–7.5 mm long, 5.2–6.5, obovate; plants of the Mohave desert region of SW Utah and southward . . . . *L. fremontii*

— Silicles 2.3–2.6 mm long, 1.8–2.2 mm wide; plants montane, in Uintah County, Utah. . . . . *L. huberi*

This taxon, a definite subshrub, differs from *L. montanum* Nutt. sens. lat. in about the same degree and manner that the Mohavaean desert *L. fremontii* Wats. differs from that species complex, i.e., in degree of woodiness and in size of the silicles, which in *L. fremontii* are on the large size for that complex and in *L. huberi* are smaller. Members of the *montanum* complex are widely distributed in the American West and occur in an array of morphological races, many of which are geographically or edaphically correlated. Hitchcock (1936) treated 13 infraspecific taxa, some of which are now regarded at specific rank. The phase of the *L. montanum* complex that is apparently most closely allied to montane *L. huberi* is the extralimital var. *alyssoides* (Gray) Jones, to which early collections of this novelty were assigned. That variety, which ranges widely from Colorado to New Mexico, Arizona, and Texas, sometimes has a branching subligneus caudex, but is seldom if ever subshrubby, and lacks the other morphological features of *L. huberi*. The spatially and elevationally isolated var. *spathulatum* (Robinson) C. L. Hitchc., also an ally, is rather common in Uintah County and elsewhere in eastern Utah. It is a tall plant, apparently biennial or short-lived perennial, with a single stem from the base, the caudex not woody or much branched. It is most common at low elevations along drainages, growing with sagebrush. Most phases within the *montanum* complex have been regarded at specific rank in the past, and there is more than marginal justification for so treating them in the future. Justification for regarding *L. huberi* at specific rank involves its combination of morphological characters, i.e., long-lived perennial habit, ligneus base, deeply lobed lower cauline leaves, and small silicles.

Lepidium huberi grows in sand or silty sands derived from formations of various age from the Shinarump Member of the Chinle, Park City, and Weber Sandstone, all on the south-plunging flank of the Uinta Mountains. It occurs in black sagebrush, mountain brush, ponderosa pine, lodgepole pine, and spruce-fir communities at 2225 to 2960 m elevation.

Artemisia nova A. Nels. var. *duchesnicola* Welsh & Goodrich, var. nov.

Persimilis *Artemisia nova* A. Nels. in magnitudine et habitu sed in folius pilis albis dense non-glanduliferis et in floribus generaliter 5 (raro 4) et bracteis plus numerosis (10–20, nec 8–12) differt (Fig. 2).

Shrubs, 1–3 (5) dm tall, main branches spreading, vegetative stems 1–3 dm long (rarely more); flowering stems mainly 1.5–3 (4) dm long; leaves dimorphic, 0.3–2 cm long, those of old stems shallowly to deeply 3- to 5-lobed or -toothed, lobes or teeth rounded, cuneate basally, appressed white canescent and not punctate; inflorescence narrowly paniculate, seldom more than 3 cm wide; involucres 3.1–5.8 mm long, 1.4–3.4 mm wide, cylindric to narrowly campanulate; bracts 10–20,

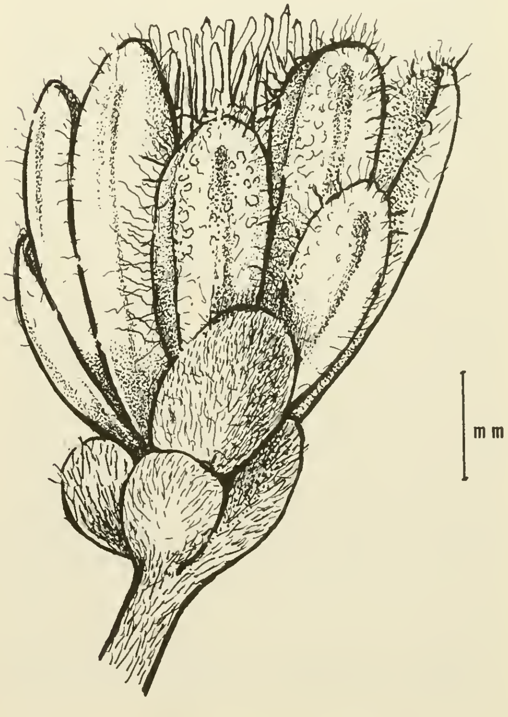

Fig. 2. Drawing of floral head of *Artemisia nova* A. Nels. var. *duchesnicola* Welsh & Goodrich.

white canescent, the margin hyaline; flowers 5 (rarely 4), all perfect; receptacle glabrous; achenes glabrous.

TYPE.—USA: Utah: Uintah County, T5S R20E S5 NE1/4, 16 km W of Vernal, 1710 m elevation, desert shrub community, on heavy, reddish clay of the Duchesne River Formation, S. Goodrich 23215, 17 Sept. 1990 (holotype BRY; isotypes to be distributed).

ADDITIONAL SPECIMENS.—USA: Utah: Uintah County, T5S R19E NW 1/4 S2, along Hwy 121, 3 km E of Lapoint, 1740 m elevation, Neese et al. 11013, 19 Sept. 1981; do, T5S R19E S2, 3 km NE of Lapoint, along Hwy 121, 1665 m, on red silty clay of the Duchesne River Formation, S. Goodrich 22225, 5 Sept. 1986; do, T1N R1E S26 SE1/4 USM, 0.6 km SE of Tridell, 1720 m, heavy clay of the Duchesne River Formation, S. Goodrich 23212, 17 Sept. 1990; do, T5S R19E S2 NW1/4, 3 km E of Lapoint, 1720 m elevation, on heavy, reddish clay of the Duchesne River Formation, S. Goodrich 23214, 17 Sept. 1990; do, T3S R19E S35 E1/2 SLM, about 1.4 km N of Hwy 121 between Lapoint and Maeser, red clays of Duchesne River Formation, 1800 m elevation, S. Goodrich 23255, 27 Sept. 1990 (all BRY, with numerous duplicates to be distributed).

This taxon differs from typical *A. nova* A. Nels. in the densely white pubescent outer involucral bracts and generally denser pubescence of leaves and flowering stalks, and in the lack of conspicuous glandular dots on leaves. Leaves are not the green to lead-gray color typical of most populations of var. *nova*, most of which also have glandular dots. There are, however, a few known populations of var. *nova* that lack glandular dots, but they possess the lead-gray to green color. In var. *duchesnicola*, the dense white, or silvery, pubescence of leaves that lack glands is diagnostic. Additionally, mature involucres of var. *duchesnicola* are less lustrous, the number of involucral bracts is greater on the average (8–12 in var. *nova*, 10–20 in var. *duchesnicola*), and the flower number is almost uniformly 5 (not 3–8 as in var. *nova*). Practically all other features of the variety proposed herein are similar to var. *nova*.

The proposed new variety would key in Welsh et al. (1993) to *A. arbuscula* Nutt. From that species var. *duschesnicola* can be distinguished by its relatively shorter flowering stems, uniformly three-lobed vegetative leaves, much larger number of involucral bracts (10–20, not 4–8), and uniformly 5-flowered heads (not 4–9).

The following key, modified from Welsh et al. (1993) will aid in identification of this taxon and its near allies.

1. Inflorescence open-paniculate, commonly more than 2 cm wide; plants often more than 5 dm tall . . . . *A. tridentata* var. *wyomingensis*

— Inflorescence narrowly paniculate, commonly less than 2 cm wide; plants usually less than 5 dm tall 2

2(1). Plants commonly 3–5 dm tall (sometimes taller); involucral bracts 4–8 . . . . *A. arbuscula*

— Plants commonly 3 dm tall or less; involucral bracts averaging more than 8 3

3(2). Vesture of plants silvery white; involucral bracts 10–20 . . . . *A. nova* var. *duchesnicola*

— Vesture of plants mainly lead-gray; involucral bracts 8–12 . . . . *A. nova* var. *nova*

The var. *duchesnicola* is the dominant plant, often in association with other desert shrubs, on reddish clay soils of the Duchesne River Formation, for which the variety is named, from about 15 km west of Vernal to Tridell. It occurs from about 1700 to 1800 m elevation on low clay uplands in a position ecologically between *A. tridentata* var. *wyomingensis* (Beetle & Young) Welsh of desert drainages and *A. nova* var. *nova*, which grows in rocky substrates formed by ancient stream pediments. Suggested as the origin of this entity is potential hybridization of *A. nova* and *A. tridentata* var. *wyomingensis*. Although differing only in minor ways, the plants are continuous and uniform over rather large expanses of the Duchesne River Formation, and they are worthy of taxonomic recognition.

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PREY CHOICES AND FORAGING EFFICIENCY OF RECENTLY FLEDGED CALIFORNIA GULLS AT MONO LAKE, CALIFORNIA

Chris S. Elphick[1] and Margaret A. Rubega[2]

ABSTRACT.—We studied the foraging biology of recently fledged California Gulls (*Larus californicus*) at Mono Lake during August–September 1991. We made behavioral observations to collect information on the relative proportions of different prey types in the diet of these birds and took plankton tows to determine the relative abundance of each prey in the water column. These data show that alkali flies (*Ephydra hians*) were the primary constituent of the diet and that they were eaten at a much higher rate than one would expect based on their abundance. We also determined the number of feeding attempts and successful captures made during each behavioral observation. From these, we calculated the birds' feeding efficiencies on emergent adult alkali flies and on all other prey types combined. We found that foraging efficiencies on emergent flies were very high and significantly greater than those obtained on other prey types. These results suggest that flies were actively sought in preference to the alternative prey type, brine shrimp (*Artemia monica*), presumably because they are easier to capture and of greater nutritional value.

Key words: California Gull, Larus californicus, *diet, foraging efficiency, Mono Lake.*

California Gulls (*Larus californicus*) breed widely in the arid West, with the largest concentrations at two saline lakes: Great Salt Lake in Utah and Mono Lake in east central California (Conover 1983). Various factors may influence the size and reproductive success of the California Gull colony at Mono Lake: predation, food supply, weather, parasitism, nesting habitat, and access to freshwater (Winkler 1983, Winkler cited in Botkin et al. 1988). Of these, increased risk of predation caused by the exposure of a "land-bridge" between the mainland and islands on which the birds breed has received most attention (Patten et al. 1987, Botkin et al. 1988).

The role of food abundance has received relatively little discussion, primarily because information on the diet of California Gulls at Mono Lake is limited. Brine shrimp (*Artemia monica*) and alkali flies (*Ephydra hians*) are the main sources of food available to gulls, although other items (e.g., cicadas, fish, and garbage) are occasionally taken (Patten et al. 1987). Previous reports have focused on the food brought to chicks at the nest. Some of these studies show chick diets to be dominated by brine shrimp (Grinnell and Storer 1924, Winkler et al. 1977, Jehl and Mahoney 1983), while others found high proportions of alkali flies (Nichols 1938, Young 1952, Mason 1967). Diet data for other age classes of gulls are not widely available. Young (1952) dissected two individuals and found their guts to be full of alkali fly pupae, and Jehl and Mahoney (1983) found high proportions (>90% by volume) of shrimp in a sample of free-swimming gulls (18 adults, 20 fledglings). These studies show that both brine shrimp and alkali flies are used by California Gulls at Mono Lake under certain circumstances. The factors that determine which of the two prey species, or which life stages of alkali flies, are taken are not known. Do the patterns simply reflect variation in relative abundances of prey species, or is one species preferred but not always available?

During three summers of fieldwork we noticed that over the latter part of summer California Gulls feed extensively on alkali flies, particularly recently emerged adults. Flies of this age class are immotile and presumably easier to catch than either brine shrimp or fly larvae (though not necessarily fly pupae). We therefore hypothesized that they would be a preferred prey source when available. In this paper we quantify the incidence of alkali flies in the diet of recently fledged California Gulls.

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We restricted our study to juvenile gulls because inexperienced birds are typically the least proficient foragers (Porter and Sealey 1982, Burger 1987, Wunderle 1991) and hence most likely to benefit from the availability of easily captured prey. We demonstrate that under certain circumstances alkali flies (1) constitute a major proportion of the diet and (2) are not eaten in direct proportion to their abundance. As a potential explanation for the birds' apparent preference for alkali flies when available, we also test the hypothesis that fledgling gulls are able to achieve greater feeding efficiencies when eating emergent adult flies than when foraging on alternative prey.

METHODS

Data were collected on five days during August and September 1991 from waters just off the northeastern shore of Mono Lake, where feeding gulls were numerous.

FEEDING OBSERVATIONS.—We obtained feeding data by videotaping foraging birds with a Sony 8 mm HandyCam video recorder with an 8X zoom lens ($n = 50$) or by direct observations ($n = 20$). In all cases the focal bird was within 10 m of the observer, and foraging behavior was scored over a 1-min feeding trial. No more than 10 birds were observed at any site to reduce the chance of obtaining repeated samples of the same individual.

Feeding trials were scored for the number of feeding attempts and successful captures, which were divided by one minute to give attempt and success rates. When possible, prey items were identified. An attempt was defined as any occasion on which the bird's bill entered the water or the bird lunged for a prey item on the water's surface. Attempts were deemed successful if (1) the gull was seen "head-throwing" (i.e., inertial feeding; Gans 1961) and swallowing after the attempt, (2) the prey item was observed in the bird's mandibles and not dropped, or (3) the prey item was visible on the water surface before the capture attempt and was picked off by the gull. Filmed trials were scored at half-speed to improve accuracy. Data from the one day when both methods were used were compared to assess the relative accuracies of videotaping and direct observation.

DIET.—We used two measures to determine the incidence of alkali flies in the diet of juvenile gulls. First, we used the number of attempts directed at flies (all life stages), divided by the total number of attempts, as a measure of the proportion of foraging effort directed at alkali flies. Second, we calculated the minimum proportion of the birds' diet that constituted flies:

$$\frac{\text{fly captures}}{\text{attempts on all prey minus known failures.}}$$

PREY ABUNDANCE.—Prey abundance was determined from horizontal plankton tows taken at the site of, and immediately after, a series of feeding trials. Tows were made with a 0.5-μm mesh plankton net, 1 m in diameter, and supported at the surface by floats. The tows sampled approximately 6 m^3 of water, down to a maximum depth of about 60 cm. Samples were sorted and individuals of each alkali fly life stage counted. Because shrimp were too numerous to count, their numbers were calculated from a previously determined wet weight to number relationship (Rubega unpublished data):

$$\text{Weight (g)} = 0.002207 * \text{Number } (r^2 = .96, n = 10).$$

FEEDING EFFICIENCY.—We calculated feeding efficiency of juvenile gulls by dividing the number of successful prey captures by the number of attempts for both emergent adult alkali flies and all other prey types combined. These values were compared using a paired t test in which the two efficiency measures for each individual were paired. Feeding efficiency could not be calculated individually for other prey types because, unlike adult flies, they occurred below the water's surface and often could not be seen unless they were captured. Hence, usually we were unable to determine the object of the foraging attempt unless the attempt was directed at an adult fly. All estimates are given in means (± standard error).

RESULTS

Table 1 compares the minimum proportions of the total diet for each prey type with the relative abundances of each prey in plankton tows. Alkali fly adults and pupae both were eaten in much higher numbers than expected if prey were taken in proportion to their abundance. The minimum proportion of

TABLE 1. Mean proportions (± SEM) of different prey types in the diet of fledged California Gulls ($n = 70$) and in plankton tows taken where birds were feeding ($n = 21$). No diet data are available for fly larvae or shrimp because they could not be distinguished in our feeding trials.

Prey type	Abundance in diet (% by number)	Abundance in plankton tows (% by number)
Alkali fly adults	≥ 22.59 ± 0.35	0.01 ± 0.003
Alkali fly pupae	≥ 18.20 ± 0.39	0.67 ± 0.40
Alkali fly larvae	—	0.05 ± 0.0007
Alkali flies (all life stages)	≥ 40.79 ± 0.36	0.74 ± 0.04
Brine shrimp	—	99.25 ± 0.04

foraging attempts directed at flies (all life stages) and the minimum proportion of the diet comprised of flies were 41.7 ± 3.0% and 40.8 ± 3.0%, respectively ($n = 70$). In comparison, only 0.7 ± 0.8% ($n = 22$) of prey items sampled in the water column were alkali flies; the remainder were all brine shrimp. These data indicate that alkali flies were favored over brine shrimp.

The two sampling methods are compared in Table 2a. Attempt and success rates for all prey types combined did not differ significantly between the videotaped feeding trials and those obtained by direct observation ($t_{33} = -0.1$, $P = .933$ and $t_{33} = 1.56$, $P = .128$, respectively). Proportions of different prey types recorded did differ, however, with videotaped trials, underrecording the number of pupae captured by an average of 79.7% on the one day for which a comparison was possible. Similar numbers of adult flies were detected by the two methods. This discrepancy was probably because, unlike adult flies, pupae do not float on top of the water surface and are difficult to see on film due to reflection. Values given above for the incidence of alkali flies in the diet are therefore underestimates.

Mean foraging efficiency for recently fledged gulls feeding on emergent alkali flies was very high and significantly greater than mean efficiency on all other prey (Table 2b; paired $t_{45} = 10.8$, $P < .0001$). In addition, a comparison of the two measures for each individual showed that in all but one case a bird's efficiency was greater when feeding on emergent flies. Although our foraging efficiency data for alkali fly pupae are limited because we did not always know what prey type an attempt was directed at, they do indicate that pupae were caught as easily as adult flies (Table 2a).

DISCUSSION

The large difference between alkali fly use and abundance strongly suggests that flies were actively sought in preference to brine shrimp and that flies were an important component in the diet of the birds we observed. It is likely that our prey sampling regime underestimated the availability of alkali flies because (1) we sampled deeper in the water column than gulls forage and (2) emergent flies are most abundant at the surface. It is unlikely, however, that this could account for the 60-fold difference between observed and expected values for fly abundance in the birds' diet. Two factors may contribute to the apparent preference for flies over shrimp. First, we have shown that 27% higher foraging efficiencies can be attained when feeding on emergent alkali flies than on alternative prey types combined. Second, Herbst (1986) reported that alkali flies are larger and have a greater nutritional value than the alternative food, brine shrimp. Both factors mean that there is an increase in food intake per unit effort when feeding on emergent flies. Although we have no quantitative data for adult gulls, observations made during the course of this study suggest that they also fed predominantly on alkali flies. A supply of easily caught prey, however, would be expected to benefit juveniles more that adults because the former lack foraging experience and are more likely to have difficulty feeding on more motile prey.

Conclusions that can be drawn from these results are obviously limited. Our sampling was restricted to a few dates in one year and one portion of Mono Lake. Our anecdotal observations from two additional years and surveys conducted across the entire lake suggest that these findings are not atypical for late summer, when emergent flies and dislodged pupae are common at the water surface. We have no data for other time periods; however, chick diet data collected earlier in the summer suggest that flies were eaten throughout the post-hatching period in 1991 (D. Shuford personal communication). Jehl and Mahoney's (1983) data clearly show that under some circumstances brine shrimp make up a major portion of the diet of fledgling California Gulls. The difference between their result and ours mirrors the variation seen in the diet of chicks (Grinnell and Storer 1924, Nichols 1938, Young 1952,

TABLE 2. Mean feeding performance values (± SEM). Sample sizes given in parentheses. (a) Comparative values for the two observation methods from the one day on which both were used. (b) Values for the two prey classifications for which accurate data could be collected from all study days.

Prey type	Attempt/min	Success/min	Efficiency (%)
(a) Comparison of observation methods			
Alkali fly adults (video trials)	0.53 ± 0.06 (15)	0.53 ± 0.06 (15)	100 ± 0 (5)
Alkali fly adults (direct observation)	0.65 ± 0.05 (20)	0.65 ± 0.05 (20)	100 ± 0 (8)
Alkali fly pupae (video trials)	2.40 ± 0.31 (15)*	1.93 ± 0.286 (15)	81.75 ± 0.03 (8)*
Alkali fly pupae (direct observation)	9.50 ± 0.22 (20)*	9.50 ± 0.22 (20)	100 ± 0 (20)*
All prey (video trials)	16.67 ± 0.43 (15)	13.07 ± 0.40 (15)	78.25 ± 0.85 (15)
All prey (direct observation)	16.85 ± 0.31 (20)	10.15 ± 0.25 (20)	59.00 ± 0.90 (20)
(b) Comparison of prey types			
Alkali fly adults	8.30 ± 0.15 (70)	7.79 ± 0.14 (70)	95.77 ± 1.0 (70)
All prey except adult flies	17.20 ± 0.99 (70)	11.99 ± 0.09 (70)	68.40 ± 0.23 (70)

*These data should be viewed with caution as attempt rates are minimums.

Mason 1967, Winkler et al. 1977, Jehl and Mahoney 1983). Alkali fly abundance varies seasonally with an increase during May and June, peak numbers between July and September, and a gradual decline thereafter (Herbst 1986). Research by Point Reyes Bird Observatory shows that the relative proportions of flies and shrimp in food brought to chicks differ considerably between samples collected during the day and night, and between years (D. Shuford personal communication). These observations not only suggest that relative availability of the two prey is quite variable at daily, seasonal, and annual time scales but also help explain the discrepancies between studies. Previous diet studies did not present data on relative prey abundances in areas where birds were foraging. In demonstrating a higher than expected abundance of alkali flies in the diet of fledgling gulls and the high foraging efficiencies that can be attained when feeding on them, our study suggests that flies are the preferred prey when they are available.

In light of recent research on Red-necked Phalaropes (*Phalaropus lobatus*), which are physiologically unable to survive on a diet of pure brine shrimp (Rubega and Inouye 1994), our data lead us to speculate that brine fly production may be an important factor in determining fledgling survival rates (currently unknown) for the Mono Lake gull colony. California Gulls clearly eat brine shrimp on a regular basis and apparently are not as dependent on alkali flies as Red-necked Phalaropes. However, it is not clear whether the prey supply is limiting the gull population size. Experiments needed to address that issue have yet to be performed. In addition, it is possible that gull predation plays an important role in determining alkali fly recruitment rates. The extent to which these issues are important can only be established through further study of the interactions between flies and gulls, both at Mono Lake and elsewhere.

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HYBRIDIZATION BETWEEN *BUFO WOODHOUSII* AND *BUFO PUNCTATUS* FROM THE GRAND CANYON REGION OF ARIZONA

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Key words: hybridization, Bufo woodhousii, Bufo punctatus, *toads, Anura, distribution.*

Natural hybridization between toads of the genus *Bufo* is common; most accounts involve representatives from the same species group (Sullivan 1986). Species groups within the genus *Bufo* are hypothesized to be monophyletic groups, based on data that include osteology, lab hybridization studies, advertisement calls, and release calls (summarized in Blair 1972a). Intergroup hybrid adults are expected to be relatively more rare in nature because of the low proportion that develop completely (Blair 1972b). Here we report intergroup hybridization between *Bufo woodhousii* (*americanus* group) and *Bufo punctatus* (*punctatus* group; Blair 1972c). Hybrid *B. punctatus* × *B. woodhousii* previously reported from Colorado near Grand Junction were described as "sterile males with atrophied testes" (McCoy et al. 1967). We present evidence that *B. woodhousii* and *B. punctatus* have hybridized at two new localities in Arizona, Coconino Co., and that atrophied testes are not universal in these hybrids. The localities are approximately 3 km upstream from the Colorado River, near Powell Canyon in the Little Colorado River Gorge, and approximately 8 km downstream of the confluence of the Little Colorado River and Colorado River where Lava Creek empties into the Colorado River. We also analyzed specimens collected by S. W. Aitchison in 1973 from Choal Canyon, Coconino Co., approximately 22.5 km NNE of Kaibito; these specimens include putative hybrid *B. punctatus* × *B. woodhousii*. Hybrids from this series are likely the toads that support the comment by Miller et al. (1982) that hybridization between *B. punctatus* and *B. woodhousii* occurs in Grand Canyon National Park.

Toads were identified and analyzed morphologically using methods similar to those of Ferguson and Lowe (1955) and McCoy et al. (1967). Each toad was dissected to determine sex and condition of testes of putative hybrids. Twelve specimens from the Little Colorado River (LCR) site [3 *B. punctatus* (ASU28935-28937), 8 *B. woodhousii* (ASU28939-28946), and the hybrid (ASU28938)], and 15 of the 17 specimens from Choal Canyon (CC) [8 *B. punctatus* (MNA Z6.529-536), 5 *B. woodhousii* (MNA Z6.522-526), and 2 hybrids (MNA Z6.527-528)] were analyzed. The two toads from Choal Canyon excluded from the analysis were too small to evaluate reliably since ontogenetic changes in cranial crest and parotoid gland morphology occur in some toads (Sullivan 1986). Measurements were taken from preserved male toads that were all the size of reproductively mature individuals. A Helios vernier caliper precise to 0.05 mm was used. Body size and parotoid gland variation among species of toads are diagnostic for many species. For the toads we examined, *B. woodhousii* is larger and has more elongate parotoid glands than *B. punctatus*, which is a smaller toad with small, round parotoid glands. We measured snout-vent length (SVL) and parotoid gland length (PL) and width (PW). A ratio of parotoid gland dimensions (PL/PW) was formed to evaluate gland shape.

All toads from the LCR collection have developed gonads and secondary sexual characteristics. The three *B. punctatus* and four *B. woodhousii* males exhibit darkened vocal sacs, well-developed thumb pads, and testes typical for the species. The other four *B. woodhousii* appear to be spent females containing ovaries

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with undeveloped eggs. The hybrid male possesses one typical looking testis and one greatly enlarged testis, approximately 10 times normal size.

Morphological analysis supports identification of ASU28398 as a hybrid. Values presented are the mean ± SD. The hybrid was 58.80 mm SVL, larger than *B. punctatus* (42.17 ± 1.48 mm) but similar in size to *B. woodhousii* (59.69 ± 6.03). Shape of the parotoid gland, PL/PW, was intermediate for the hybrid, 1.43, relative to *B. punctatus* (1.017 ± 0.053) and *B. woodhousii* (2.161 ± 0.330; Fig. 1). Both PL/PW and SVL are different between the species with at least 95% confidence because the means ± 2STD do not overlap.

Although no specimens were retained from the Lava Creek site (LC), photographs taken in April 1993 provide clear evidence of hybridization between *B. punctatus* and *B. woodhousii* at this second site in Grand Canyon National Park (Fig. 2). Body size, parotoid gland morphology, and coloration of the adult male hybrid are intermediate. *Bufo woodhousii* is larger, has much more elongate parotoid glands, and lacks the spinose red warts seen in *Bufo punctatus*.

We submit this photographic evidence and morphological analysis of toads as support for the suggestion by Stevens (1983) that *B. punctatus* × *B. woodhousii* hybrids occur in the Grand Canyon region of Arizona. We also suggest that, based on specimens not from the Grand Canyon region, but from specimens collected associated with Glen Canyon, Miller et al. (1982) reported that *B. punctatus* × *B. woodhousii* hybrids occur in the Grand Canyon. Whether *B. punctatus* × *B. woodhousii* hybrids from LCR and LC could reproduce would require histological analysis and additional sampling to determine if hybrids have viable sperm. We are, however, unaware of other reports of enlarged testes in hybrid toads.

Three toads from Choal Canyon, MNA Z6.527-528 and MNA Z6.496, may be hybrids based on intermediate values of PL/PW (1.42 ± 0.04). As in the LCR series, SVLs of hybrids (58.01 ± 3.37) are greater than *B. punctatus* (48.84 ± 6.17), but similar to *B. woodhousii* (56.02 ± 7.87; Fig. 1). The means ± 2STD for SVL and PL/PW overlap for the CC sample; therefore, significant statistical differences do not exist. A small sample size is likely influential. Gonadal development in some CC hybrids is unusual; MNA Z6.496 could not be sexed by its gonads or secondary sexual characters. The other two hybrids, MNA Z6.527 and 528, have darkened thumb pads and vocal sacs. Both testes of MNA Z6.527 appear normal, but MNA Z6.528 has one enlarged testis and the other absent or greatly reduced. Again, whether hybrid males of this cross are reproductively functional is unknown.

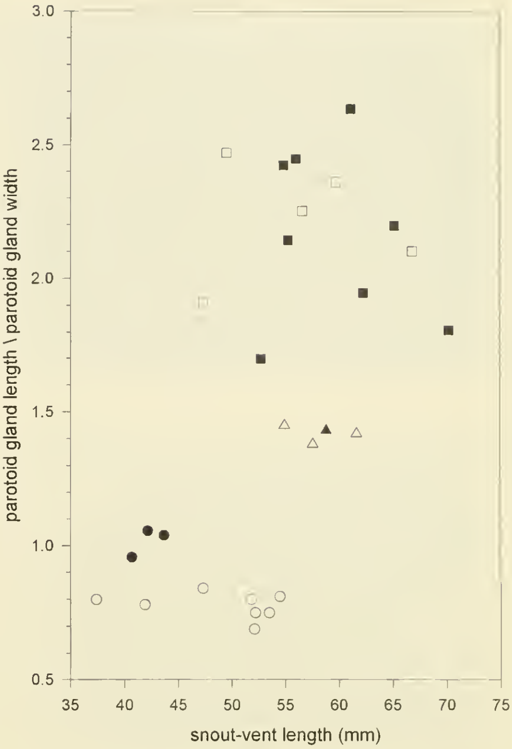

Fig. 1. Comparison of relative sizes and parotoid gland dimensions of specimens from the Little Colorado River locality (closed symbols) and the Choal Canyon locality (open symbols). Circles are *Bufo woodhousii*, squares are *Bufo punctatus*, and triangles are hybrids.

Field observations suggest that hybridization at LCR may be relatively common. When the LCR collection was obtained, 13–14 May 1993, advertisement calls typical of *B. woodhousii* and *B. punctatus* were both heard at night, as well as calls that sounded aberrant, approximately intermediate in duration, pulse rate, and pitch of each species. No other species of toads were observed during spring months

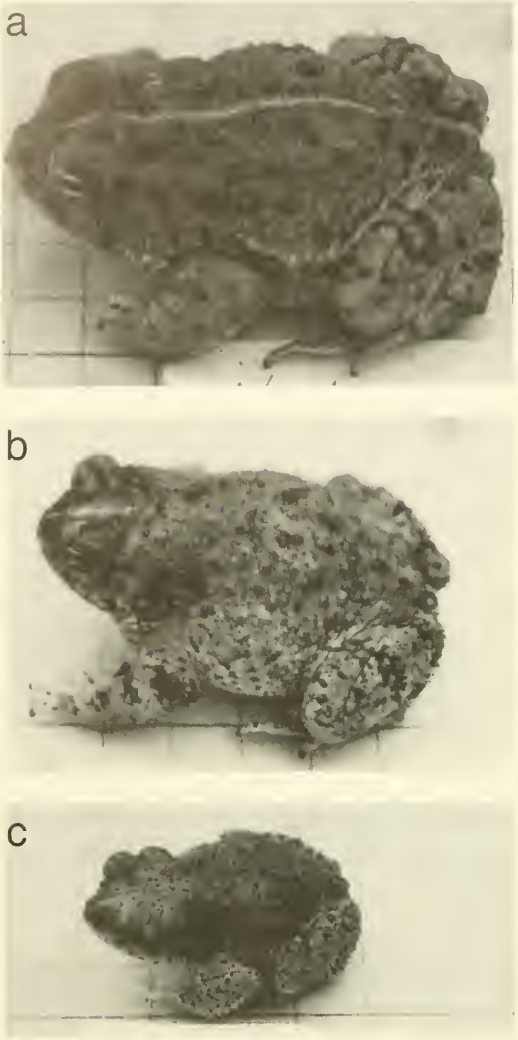

Fig. 2. Photographs of toads from the Lava Creek locality: (a) *Bufo woodhousii*, (b) hybrid, (c) *Bufo punctatus*.

at the LCR site for two years. Advertisement calls produced by hybrid toads often have characteristics intermediate to their parental forms (Blair 1956, Zweifel 1968, Sullivan 1986, 1990). Calls of suspected hybrids were not heard at Lava Creek, but both species chorused together there in April 1993.

Habitat disturbance and environmental change associated with Glen Canyon Dam may contribute to hybridization between these taxa in the Grand Canyon region. Other hybrid zones between toads are associated with river regulation projects or human impacted areas (Sullivan 1986 and examples cited therein). Alterations to the Colorado River have reduced seasonal peak flows, created large daily fluctuations in flow, and dramatically lowered the temperature of the water. Tributaries such as the Little Colorado River and Lava Creek are relatively less affected. Perhaps departure from historic conditions contributes to the likelihood of contact and hybridization between *B. woodhousii* and *B. punctatus* in the Grand Canyon. Other possible explanations for hybridization include natural perturbations that disrupt ecological separation. Also, natural cycles in population size and species range are hypothesized to account for many hybrid zones (Hewitt 1989).

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We thank M. E. Douglas at Arizona State University and M. Morales and D. Hill at the Museum of Northern Arizona for use of specimens. We thank B. K. Sullivan for suggestions on the manuscript. We also thank the Navajo Fish and Wildlife Branch of the Navajo Nation for providing a collecting permit to RNR (#930709-058). Arizona State University–West provided funds to KBM for some costs associated with this project.

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REPRODUCTION IN THE BANDED SAND SNAKE, *CHILOMENISCUS CINCTUS* (COLUBRIDAE), FROM ARIZONA

Stephen R. Goldberg[1]

Key words: Chilomeniscus cinctus, *banded sand snake, Colubridae, reproduction, Arizona.*

The banded sand snake, *Chilomeniscus cinctus* Cope, 1861, ranges from central Arizona to extreme southern Sonora, and throughout all but the northern part of Baja California (Stebbins 1985). Anecdotal comments on the reproduction of this species have been published in Stebbins (1954), Wright and Wright (1957), and Behler and King (1979), and in this report I provide data on reproduction in *C. cinctus* from Arizona.

I examined 38 *Chilomeniscus cinctus* (24 males, 14 females) from Arizona in the herpetology collections of Arizona State University (ASU), Tempe; Natural History Museum of Los Angeles County (LACM), Los Angeles; San Diego Natural History Museum (SDSNH), San Diego; and the University of Arizona (UAZ), Tucson. Museum numbers of specimens examined are given in Appendix 1. All Arizona *C. cinctus* in the above collections were examined; however, some had been damaged (road-kills) or had not been preserved promptly enough to avoid autolysis. These were not used and are not in Appendix 1. Counts were made of oviductal eggs or enlarged follicles. The left gonad was removed for histological examination, embedded in paraffin, and cut into histological sections at 5 μm. Slides were stained with Harris' hematoxylin followed by eosin counterstain. Testes slides were examined to determine the stage of the male cycle; ovary slides were examined for the presence of yolk deposition.

Data on the male *C. cinctus* seasonal testicular cycle are presented in Table 1. Testicular histology was similar to that reported in Goldberg and Parker (1975) for two other North American colubrid snakes, *Masticophis taeniatus* and *Pituophis melanoleucus*. In the regressed testes, seminiferous tubules contained spermatogonia and Sertoli cells. In recrudescence, there was renewal of spermatogenic cells characterized by spermatogonial divisions; primary and secondary spermatocytes, and spermatids, may have been present. In spermiogenesis, metamorphosing spermatids and mature sperm were present.

Small sample sizes from all months except May–June (Table 1) prevented a definitive description of the male cycle. However, since all 10 May males and 5 June males were undergoing spermiogenesis, it is likely that *C. cinctus* breeds during these months. Epididymides from 2 May and 1 June males contained sperm. The smallest spermiogenic male (sperm present) measured 151 mm in snout-vent length (SVL).

Data on the *C. cinctus* seasonal ovarian cycle are presented in Table 2. I recorded two clutch sizes: 6 June, 3 enlarged follicles (3–4 mm diameter), 188 mm in SVL; 4 July, 2 oviductal eggs (6 mm diameter), 192 mm in SVL. Yolk deposition (vitellogenic granules) was found on histological examination of ovarian

TABLE 1. Monthly distribution of conditions in seasonal testicular cycle of *Chilomeniscus cinctus*. Values shown are the numbers of males exhibiting each of the three conditions.

Month	*N*	Regressed	Recrudescence	Spermiogenesis
January	1	0	0	1
February	1	0	1	0
March	2	0	1	1
April	2	0	0	2
May	10	0	0	10
June	5	0	0	5
July	1	1	0	0
September	1	1	0	0
December	1	0	1	0

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TABLE 2. Monthly distribution of conditions in seasonal ovarian cycle of *Chilomeniscus cinctus*. Values shown are the number of females exhibiting each of the four conditions.

Month	*N*	Inactive	Yolk deposition	Enlarged follicles	Oviductal eggs
February	1	1	0	0	0
March	1	1	0	0	0
April	2	2	0	0	0
June	4	1	2	1	0
July	2	1	0	0	1
August	1	1	0	0	0
September	1	1	0	0	0
October	1	1	0	0	0
November	1	1	0	0	0

tissue from two June females (173 mm and 198 mm in SVL). No yolk deposition was seen in the remainder of the female sample. The lack of vitellogenesis in some adult females during the reproductive season may indicate that not all *C. cinctus* females breed each year. Breeding by only part of the adult female population has been reported for other North American temperate zone snake species (see Aldridge 1979). The smallest reproductively active female (yolk deposition in progress) measured 173 mm in SVL.

The biology of *C. cinctus* is poorly known. A few reports on its food habits reveal that it eats centipedes and insects (Vorhies 1926, Stebbins 1954, 1985, Behler and King 1979). According to Lowe et al. (1986), *C. cinctus* has grooved rear teeth; it is not known whether it has toxic gland secretions. The small numbers of *C. cinctus* in the two major Arizona herpetology collections (ASU, UAZ) reflect the secretive nature of this snake. Intensive study will be required before the biology of *C. cinctus* is known.

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APPENDIX 1

Specimens examined by county from herpetology collections at Arizona State University (ASU), Natural History Museum of Los Angeles County (LACM), San Diego Natural History Museum (SDSNH), and University of Arizona (UAZ).

Maricopa: ASU 04669, 09161, 13903, 26367-26368. LACM 112460. UAZ 24104, 35645, 35795, 35818. **Pima:** SDSNH 33383. ASU 01231, 15391, 28401. LACM 34918. UAZ 24087, 24089, 24092, 24095-24096, 24103, 24107-24108, 30241, 33815, 34411, 34680-34681, 35166, 36108, 37819, 37821, 42197. **Pinal:** ASU 15376, 23573, 26411, 26413. UAZ 24097.

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NO ACOUSTIC BENEFIT TO SUBTERRANEAN CALLING IN THE CICADA *OKANAGANA PALLIDULA* DAVIS (HOMOPTERA: TIBICINIDAE)

Allen F. Sanborn[1] and Polly K. Phillips[2]

Key words: cicada, acoustic behavior, calling, sound pressure level, predator avoidance, Okanagana pallidula.

Most male cicadas produce a loud calling song to attract their mates. Sound pulses are produced when specialized muscles buckle the rib-strengthened chitinous membranes, the timbals, located on the dorsolateral surface of the first abdominal segment. Sound pulses are then modified by several body components (Pringle 1954, Bennet-Clark and Young 1992) before being radiated through the tympana (Young 1990).

Male cicadas generally use an accessible perch from which they advertise their presence to conspecific females. We came across an exception to this behavior south of Lone Pine, Inyo County, CA, on 15 July 1994. We encountered the cicada species *Okanagana pallidula* Davis singing in a scrub habitat. As we began collecting, we noticed that one individual continued to sing as we approached and was very difficult to locate on the plant. By circling the plant we found that the sound was actually coming from the ground near the base of the plant and not from on the plant itself. After clearing some grass we could see a hole about 1 cm in diameter from which the sound emanated. Within the hole we could see the head of a cicada that was calling from this subterranean site.

We measured intensity levels from males calling from burrows and from plants to determine if there is an acoustic benefit for the cicadas calling in burrows. Peak sound pressure levels (SPL) were recorded with a Brüel & Kjaer 2235 SPL meter, a Type 4155 1/2″ prepolarized condenser microphone, and a UA 0237 wind screen. The system had been calibrated with a Brüel & Kjaer 4230 portable sound pressure calibrator. The SPL meter was used in the linear frequency mode. The peak setting has a time constant of less than 100 ms and was used to ensure that rapid sound transients were measured. Measurements were made perpendicular to the long body axis with the apparatus oriented medially along the dorsal surface of a singing cicada at the thorax-abdomen junction or directly above the hole in which a cicada was singing. This procedure minimized any inconsistencies between readings due to possible asymmetries in the sound field produced by cicadas (Aidley 1969, MacNally and Young 1981). Each intensity measurement was made at a distance of 50 cm. The distance was kept constant by placing a 1/4″ (6.5 mm) dowel, attached to the SPL meter, near a calling cicada. If the cicada was disturbed by placement of the SPL meter, the reading was made only after the normal calling pattern had been reestablished. All intensity measurements are relative to 1×10^{-16} W/cm^2.

Power output was determined using the following equation:

$$Q = 4\pi r^2(I)$$

where Q = sound power (W), r = distance from source in cm (= 50 cm), and I = intensity reading for the individual (dB). Since intensity is measured on a logarithmic scale, all intensity measurements (dB readings) were converted to pressure levels (W/cm^2) prior to calculating the statistics. Mean power output was then used to calculate mean sound intensity at 50 cm for each species.

Intensity measurements are summarized in Table 1. SPL values recorded for cicadas calling from within a burrow are lower than values recorded when the animals were calling from a plant; however, the values are not significantly different ($t = 1.49$, d.f. = 3, $P = .1159$). A greater number of trials may provide

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TABLE 1. Intensity of *Okanagana pallidula* calling songs. Song power was calculated from individual measurements. Mean power was used to determine the mean sound pressure level for each perch. Measurements are relative to 1×10^{-16} W/cm^2.

Location of calling perch	Sound power (mW)	Mean intensity (dB)	Range (dB)
Exposed calls	1.106 ± .6823 (n = 3)	85.46	83.4–87.8
Subterranean calls	0.340 ± .1190 (n = 2)	80.34	79.1–81.3

the statistical significance. We were unable to find a large number of individuals singing from burrows. Similarly, the vast majority of specimens calling from plants did not permit our approach to a distance necessary to collect a greater number of intensity measurements.

Subterranean calling has been described for the cicadas *O. pallidula* (Davis 1917, 1930, 1944, Beamer and Beamer 1930) and *O. vanduzeei* (Distant) (Beamer and Beamer 1930). Crickets have also been shown to call from burrows (Bennet-Clark 1970, 1987, Ulagaraj 1976, Forrest 1983, Kavanaugh 1987, Walker and Figg 1990); however, burrows fashioned by crickets increase the intensity level of their song (Bennet-Clark 1987). Subterranean calling in *O. pallidula* appears to decrease song intensity rather than increase sound transmission.

Subterranean calling may function as a predator avoidance behavior in *O. pallidula*. The difficulty we had in extracting a cicada from its burrow supports this assumption for vertebrate parasitoids. Burrows appear to be connected to nymphal development chambers, which can reach a depth of 2 ft (61 cm; Beamer and Beamer 1930). They represent a relatively safe location from which to call and may provide protection from acoustically orienting parasitoids. Many predators have been shown experimentally to orient to the calls of cicadas (Soper et al. 1976) and other acoustic insects (Walker 1964, Cade, 1975, Mangold 1978, Bell 1979, Buchler and Childs 1981, Sakaluk and Belwood 1984, Fowler and Kochalka 1985, Tuttle et al. 1985, Belwood and Morris 1987). The protective value provided against dipteran or other parasitoids to cicadas calling from burrows remains to be determined.

The majority of the population appears not to call from a burrow as indicated by the proportion of individuals we found calling from plants versus those calling from burrows. Perhaps the benefits of a protected calling site limit the chances of a male to attract a female successfully. The males may eventually abandon their burrows to increase the chances of interacting with females. It would be interesting to investigate the ontogeny of subterranean calling in cicadas.

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BOOK REVIEW

Natural History of the Colorado Plateau and Great Basin. K. T. Harper, L. L. St. Clair, K. H. Thorne, and W. M. Hess, editors. University Press of Colorado, Niwot, CO. 1994. 294 pp. $24.95 hardback.

Natural History of the Colorado Plateau and Great Basin, a multi-authored volume, is an introduction to the spectacular arid and remote North American landscape known as the Colorado Plateau and the Great Basin. The high, windswept plateau country is interrupted by numerous rocky canyons and arid valleys, and the Great Basin is a huge arid depression with no external drainages. According to the editors, this region is within the boundaries of Nevada, Utah, and Colorado (Fig. 1.2). They indicate that the intended audience of the volume includes students and managers of the region's natural resources. The basic objective of the major eleven chapters is to provide a "ready reference to the best of recent studies that are relevant to the region." Additionally, the editors hope this volume will stimulate more research, especially on the Colorado Plateau, which is more "biodiverse and perhaps more fragile ecologically than the Great Basin."

The map in Chapter 1 of the Great Basin and Colorado Plateau indicates a smaller region than maps in Chapters 2, 5, and 9, excluding areas as far north as Oregon and as far south as California, Arizona, and New Mexico. The boundaries of the Great Basin and Colorado Plateau therefore appear mildly confusing. A consensus map or better textual description (as presented in Chapter 5) could have been included in Chapter 1.

Chapter 2 presents a rather concise and useful review of the geologic history of the Great Basin and Colorado Plateau. Chapter 3 attempts to summarize the complex climatic weather patterns in the broad context of the western United States and the globe. Anyone who has spent time in the Great Basin or Colorado Plateau knows well the unpredictable and often extreme weather patterns that have helped form the regional geomorphology. Literature citations of this chapter are very useful.

Chapter 4 reviews the extinct late Pleistocene mammals of the Great Basin. This region is rich in late Pleistocene vertebrate fossils, and the author provides a discussion of the possible causes of extinction and implications concerning present faunas. Western Great Basin archaeology in the context of regional cultural/environmental models is presented in Chapter 5. Wilde describes various prehistoric ebbs and flows of peoples for the past 12,000 years. Chapter 6 touches on the current politically controversial subject of the changes in plant communities caused by domestic livestock grazing, the most widespread land-management practice in western North America. Seventy percent of the western United States is grazed, and ecological costs have been great. The author seems to concentrate on deleterious effects of the introduction of alien plants species such as Russian thistle and cheatgrass on the Great Basin plant communities. He predicts that with continued removal of cattle, the "predators" of these plants, the ecosystem structure of the Great Basin may dramatically change in the near future.

In Chapter 7 Jackson presents an enjoyable analysis of the unique factors that have influenced modern human development of resources in the Great Basin. He traces the cultural history of the region, from the Dominguez and Escalante expeditions of the 1700s to the Mormon farmers who shaped the modern human geography of the Great Basin. As Jackson pointed out, the enduring legacy of the Great Basin is the "strange juxtaposition of religion and vice, destruction and recreation." The authors in Chapter 8 use macrofossil data from packrat (*Neotoma*) middens to reconstruct the evolutionary history of eight modern conifer species. These conifer species now occupy the montane islands of the Great Basin, and the current distribution of these trees is related to past paleoclimatic changes.

Sigler and Sigler in Chaper 9 present a very comprehensive review of the fishes of the Great Basin and the Colorado Plateau. Excellent discussions are presented for each species. However, there appear to be some errors; for example, the Big Spring spinedace is a native to the Colorado River Basin, not Lahontan, and the razorback sucker is a federally endangered species as of 1991. Additionally, if the map presented in this chapter is inclusive, then perhaps several other species could be added: Moapa dace, Moapa speckled dace, Meadow Valley speckled dace, Preston speckled dace, White River sucker, and Sonora sucker. Also, I cannot construe the meaning of the last sentence in their chapter, "that many of the species, both native and exotic, have survived in spite of [human] modifications." The fact is, at least for the Colorado River Basin, most native fishes are in serious jeopardy of extinction; they have survived, but with a very precarious hold.

Chapter 10 by Nelson attempts to cover a daunting subject, the insects of the Great Basin and Colorado Plateau. An estimated 14,000–26,000 species may occur within these boundaries. He discusses several of the better regional known taxonomic groups (stoneflies, butterflies, robber flies, and ants) to answer broad questions, such as, "What range patterns are seen in the Great Basin and Colorado Plateau?" and "Did these groups evolve in the Great Basin?" Many of the insects of this region have a widespread distribution throughout the West, and the insect fauna of the Colorado Plateau have strong affinities with the Rocky Mountains physiographic province. Warren and Harper in Chapter 11 briefly discuss elevational patterns of insects in the Great Basin and Colorado Plateau. Most of their examples, however, are higher elevational patterns of the Rocky Mountains and elsewhere, and the discussion is limited to adaptations of insects to harsh environments. Their literature review is excellent.

In Chapter 12, Mead and Bell describe the herpetofauna of the Great Basin and Colorado Plateau in the late Pleistocene and Holocene (i.e., during the past two million years, or Quaternary Period). Their comparison of modern fauna with the Pleistocene-Holocene indicates that 61% of the modern fauna is represented in the fossil record, an interesting observation considering the climatic and environmental change in association with such events as ice ages.

In Chapter 13 the editors provide recommendations for future directions of research, emphasizing the need for descriptive work. They also state evolutionary and ecological questions about the biodiversity of the Great Basin and Colorado Plateau that need urgent attention.

This little book packs in much useful information, and with its reasonable price it should appeal to all students who work or visit the Intermountain West. The editors have succeeded in presenting a good introduction to many important and conspicuous aspects of the natural history of the Great Basin and Colorado Plateau.

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THE

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INDEX

VOLUME 55 — 1995

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Great Basin Naturalist 55(4), © 1995, pp. 380–386

INDEX

Volume 55—1995

AUTHOR INDEX

Anderson, Loran C., 84
Austin, Dennis D., 267

Baker, William L., 287
Bartholomew, Breck, 282
Baumann, R. W., 124
Belk, Mark C., 183
Bodie, Walt, 181
Bowlin, W. R., 19
Brusven, Merlyn A., 352

Callahan, J. R., 89
Carter, Bernard, 169
Cates, Rex G., 29
Cieminski, Karen L., 105
Cifelli, Richard L., 304
Clements, Charlie, 188
Compton, Stephen B., 89
Crawford, John A., 284
Crompton, Clifford, 322
Czaplewski, Nicholas J., 304

DeBolt, Ann Marie, 237
DeWalt, R. Edward, 1
Dobkin, David S., 315

Ehleringer, James R., 135
Elphick, Chris S., 363

Fielding, Dennis J., 352
Flake, Lester D., 105
Flinders, Jerran T., 29
Friedman, Jonathan M., 58
Furniss, Malcolm M., 335

Geer, S. M., 19
Gerdes, Michael G., 315
Gettinger, Ronald D., 315
Goldberg, Stephen R., 372
Goodrich, Sherel, 359
Griswold, T. L., 19

Hansen, E. Matthew, 158
Harper, Kimball T. (rev.), 286
Heckmann, Richard A., 258
Hubert, Wayne A., 169

Ischinger, Lee S., 58

Johnson, James B., 335
Johnson, Jerald B., 183

Kondratieff, B. C. (rev.), 377
Kucera, James R., 92

Lesica, Peter, 142
Longland, William S., 188
Lytle, C. Mel, 164

Malmos, Keith, 368
McArthur, E. Durant, 151
McCoy, Matthew, 181
McCune, Bruce, 237
Meinke, Robert J., 249
Miller, Richard F., 37
Minshall, G. Wayne, 193
Munger, James C., 74
Muth, Robert T., 95

Nohavec, Robert D., 282

Owen, Wayne R., 117

Pelren, Eric C., 284
Phillips, Polly K., 192, 374

Qi, Ying, 258

Ratliff, Raymond D., 46
Reed, J. Michael, 342
Reed, Robert, 368
Renkin, Roy A., 201
Robinson, Christopher T., 193
Rose, Jeffery A., 37

Rose, Kenneth D., 304
Royer, Todd V., 193
Rubega, Margaret A., 363
Rushforth, Samuel R., 193

Sanborn, Allen F., 192, 374
Sandquist, Darren R., 135
Shafroth, Patrick B., 58
Shepard, W. D., 124
Shiozawa, Dennis K., 183, 213
Singer, Francis J., 201
Slichter, Todd A., 74
Smith, Bruce N., 164
Snyder, Darrel E., 95
Starrett, Bryan, 368
Stewart, Kenneth W., 1
Storz, Jay F., 78
Stricklan, Dave, 29

Taye, Alan C., 225
Taylor, ElRoy, 181
Tepedino, V. J., 19

Urness, Philip J., 267

Vickery, Robert K., Jr., 174, 177

Walford, Gillian M., 287
Welsh, Stanley L., 66, 271, 322, 359
Winward, Alma H., 151
Wolz, Eric R., 213

KEY WORD INDEX

Taxa described as new to science in this volume appear in **boldface** type in this index.

acoustic behavior, 374
Acrididae, 352
age, 183
allopolyploid, 151
alpine, 117
  vascular flora, 225
  vegetation, 225
analysis
  elasticity, 142
  multivariate, 287
aneuploidy, 174
Anura, 368
Apiosoma campanulatum, 258
aquatic invertebrates, 105
Arizona, 372
Artemisia
  arbuscula* ssp. *longicaulis, 151
  nova* var. *duchesnicola, 359
Astragalus, 117, 142
Atriplex types, 322
avian diversity, 342
avoidance
  predator, 374

backwaters, 95
banded sand snake, 372
behavior, 282
  acoustic, 374
  feeding, 192
benthic habitat, 193
benthic macroinvertebrates, 213
benthos, 213
big sagebrush browsing, 210
bioaccumulation
  metal, 164
Blue Grouse, 284
browse (browsing), 267
  big sagebrush, 210
Bufo
  woodhousii, 368
  punctatus, 368
bumblebees, 177
bundle sheath leakiness, 135

California
  bighorn sheep, 181
  Gull, 363
  Mono Lake, 363
  White Mountains, 117
Calileuctra, 124
calling, 374
candidate species, 315
carbon isotope ratio, 135
caves, 315
Celtis reticulata, 237
Ceratopogonidae, 213
Cervus elaphus, 201
chemotaxonomy, 151
Chenopodiaceae, 322
Chilomeniscus cinctus, 372
Chironomidae, 213
cicada, 374
coevolution, 188
Colorado, 287
  Green River, 95
  Plateau, 225
Colubridae, 372
competition, 117
conservation priorities, 342
Cottus bairdi, 258
Crotalus scutulatus, 282
Cyprinella lutrensis, 95

death camus, 188
defoliators, 158
demography, 142
Dendragapus obscurus, 284
density
    population, 352
description, 124
desert, 169
    ecology, 135
diatoms, 193
diet(s), 95, 363
    overlap, 95
distribution, 124, 169, 368
disturbance, 193
diversity
    avian, 342
Douglas-fir, 158
Douglas rabbitbrush, 267
Dragon local fauna, 304
drought, 352

ecological aspects, 258
ecology, 237
elasticity analysis, 142
elk
    northern Yellowstone, 201
Erythranthe, 177
escape saltation, 282
evolution, 174

fauna
    Dragon local, 304
    Wagon Road local, 304
faunal list, 335
fecundity, 117
feeding behavior, 192
fish(es), 169
    nonnative, 95
flower color mutations, 177
food source, 192
foraging, 192
    efficiency, 363
    movements, 315
forest insects, 158

Gila copei, 183
Great Basin, 249, 342
Green River, [Colorado], 95
Green River, [Utah], 95, 213
growth, 183, 237

habitat, 169
    benthic, 193
halophyte, 135
herbivory, 142
hibernacula, 315
horses, 267
host-symbiont relationship, 258
hummingbirds, 177
hybrid, 151
hybridization, 368

Idaho, 181, 237
    National Engineering Laboratory, 105
industrial wastewater, 105
Insecta, 124
interception trap, 284
invertebrates
    aquatic, 105

Larus californicus, 363
lava flows, 315
leatherside chub, 183
Leguminosae, 271
Lepidium ***huberi***, 359
Leuctridae, 124
life history, 183
livestock grazing, 142, 237, 352
longevity, 237

macroinvertebrates, 193
    benthic, 213
Mammalia, 304
matrix projection models, 142
Melanoplus sanguinipes, 352
metal bioaccumulation, 164
Mimulus, 174, 177, 249
    breviflorus, 249
    evanescens, 249
    latidens, 249
monkeyflowers, 249
Mono Lake, [California], 363
montane islands, 342
morphology, 258
mountain big sagebrush, 267
mule deer, 188, 201, 267
multivariate analysis, 287
mutations
    flower color, 177

Natural History Museum, 271
Nematoda, 213
netleaf hackberry, 237
Nevada, 151
new taxa, 359
nomenclature, 271
nonnative fishes, 95
North America, 322
North Horn Formation, [Utah], 304
northern Yellowstone elk, 201
nutritional qualities, 164

Okanagana pallidula, 374
Oligochaeta, 213
Oregon, 284
    central, 315
Orthoptera, 352
Ovis canadensis, 181
Oxytropis ***deflexa*** var. ***pulcherrima***, 271

Paleocene, 304
parturition, 181
phylogeny, 124
plant(s)
  geography, 225
  poisonous, 188
  rare, 142
Plecoptera, 124
Plecotus townsendii, 315
pollinators, 177
polyploidy, 174
population density, 352
Potamogeton pectinatus, 164
predation, 142
predator avoidance, 374
pronghorn, 201
Provo River, [Utah], 258
Ptychochelus lucius, 95
Puercan, 304

radiotelemetry, 315
range
  management, 267, 352
  winter, 267
rare plant, 142
recruitment, 237
rehabilitation, 237
relationship
  host-symbiont, 258
reproduction, 183, 372
reproductive isolation, 177
revegetation, 267
riparian vegetation, 287
river benthos, 213
Rock Wrens, 192
Rocky Mountains, 287
roost
  fidelity, 315
  sites, 315
Royal Botanic Garden, 271

sagebrush
  browsing, 210
  mountain big, 267
sago pondweed, 164
Salpinctes obsoletus, 192
salt stress, 135
sanitary wastewater, 105
Scolytidae, 335
Scrophulariaceae, 249
shrubs, 267
site characteristics, 237
sound pressure level, 374
speciation, 174, 177
stand structure, 237
streams, 169, 193
subalpine fir, 158

taxonomy, 151, 249
toads, 368
Torrejonian, 304
Townsend's big-eared bat, 315
trace element cycling, 164
trade-off, 117
trap
  interception, 284
  walk-in, 284
trapping success, 284
Trichodina tenuiformis, 258
Tridentatae, 151
Troglodytidae, 192
true mountain mahogany, 267
Tushar Mountains, [Utah], 225
tussock moth, 158

Uinta Basin, [Utah] 359
Utah, 225, 267, 359
  forests, 158
  Green River, 95, 213
  North Horn Formation, 304
  Provo River, 258
  Tushar Mountains, 225
  Uinta Basin, 359

vegetation
  riparian, 387
vulnerability, 342

Wagon Road local fauna, 304
walk-in trap, 284
Washington state, 335
wastewater
  industrial, 105
  sanitary, 105
waterfowl, 164
wetland, 213
White Mountains, [California], 117
wildfire, 193
winter range, 267
Wyoming, 169

Yellowstone National Park, 193
young-of-year, 95

Zigadenus, 188

TABLE OF CONTENTS

Volume 55

No. 1—January 1995

Articles

Life histories of stoneflies (Plecoptera) in the Rio Conejos of southern Colorado . . . . R. Edward DeWalt and Kenneth W. Stewart 1

Pollinator sharing by three sympatric milkvetches, including the endangered species *Astragalus montii* . . . . S. M. Geer, V. J. Tepedino, T. L. Griswold, and W. R. Bowlin 19

Factors affecting selection of winter food and roosting resources by porcupines in Utah . . . . Dave Stricklan, Jerran T. Flinders, and Rex G. Cates 29

Historic expansion of *Juniperus occidentalis* (western juniper) in southeastern Oregon . . . . Richard F. Miller and Jeffery A. Rose 37

Rangeland alpha diversities: Harvey Valley, Lassen National Forest, California . . . . Raymond D. Ratliff 46

Effects of salinity on establishment of *Populus fremontii* (cottonwood) and *Tamarix ramosissima* (saltcedar) in southwestern United States . . . . Patrick B. Shafroth, Jonathan M. Friedman, and Lee S. Ischinger 58

Names and types of *Hedysarum* L. (Fabaceae) in North America. . . . . Stanley L. Welsh 66

Whipworm (*Trichuris dipodomys*) infection in kangaroo rats (*Dipodomys* spp.): effects on digestive efficiency . . . . James C. Munger and Todd A. Slichter 74

Local distribution and foraging behavior of the spotted bat (*Euderma maculatum*) in northwestern Colorado and adjacent Utah . . . . Jay F. Storz 78

The *Chrysothamnus-Ericameria* connection (Asteraceae) . . . . Loran C. Anderson 84

Notes

Reproductive behavior in Merriam's chipmunk (*Tamias merriami*) . . . . Stephen B. Compton and J. R. Callahan 89

Additional records of fleas (Siphonaptera) from Utah . . . . James R. Kucera 92

No. 2—April 1995

Articles

Diets of young Colorado squawfish and other small fish in backwaters of the Green River, Colorado and Utah. . . . . Robert T. Muth and Darrel E. Snyder 95

Invertebrate fauna of wastewater ponds in southeastern Idaho. . . . . Karen L. Cieminski and Lester D. Flake 105

Growth and reproduction in an alpine cushion plant: *Astragalus kentrophyta* var. *implexus* . . . . Wayne R. Owen 117

Calileuctra, a new genus, and two new species of stoneflies from California (Plecoptera: Leuctridae) . . . . W. D. Shepard and R. W. Baumann 124

Carbon isotope discrimination in the C_4 shrub *Atriplex confertifolia* along a salinity gradient . . . . . Darren R. Sandquist and James R. Ehleringer 135

Demography of *Astragalus scaphoides* and effects of herbivory on population growth . . . Peter Lesica 142

Lahontan sagebrush (*Artemisia arbuscula* ssp. *longicaulis*): a new taxon . . . . Alma H. Winward and E. Durant McArthur 151

Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) on subalpine fir in northern Utah . . . . E. Matthew Hansen **158**

Seasonal nutrient cycling in *Potamogeton pectinatus* of the lower Provo River . . . . C. Mel Lytle and Bruce N. Smith **164**

Factors influencing fish assemblages of a high-elevation desert stream system inWyoming . . . . Bernard Carter and Wayne A. Hubert **169**

Notes

Speciation by aneuploidy and polyploidy in *Mimulus* (Scrophulariaceae) . . . . Robert K. Vickery, Jr. **174**

Speciation in *Mimulus*, or, Can a simple flower color mutant lead to species divergence? . . . . Robert K. Vickery, Jr. **177**

Fall lamb production by a California bighorn sheep . . . . Matthew McCoy, Walt Bodie, and ElRoy Taylor **181**

Age, growth, and reproduction of leatherside chub (*Gila copei*) . . Jerald B. Johnson, Mark C. Belk, and Dennis K. Shiozawa **183**

Consumption of a toxic plant (*Zigadenus paniculatus*) by mule deer . . . . William S. Longland and Charlie Clements **188**

Use of an unusual food source by Rock Wrens (Troglodytidae) . . . . Polly K. Phillips and Allen F. Sanborn **192**

No. 3—July 1995

Articles

Benthic community structure in two adjacent streams in Yellowstone National Park five years after the 1988 wildfires . . . . G. Wayne Minshall, Christopher T. Robinson, Todd V. Royer, and Samuel R. Rushforth **193**

Effects of browsing by native ungulates on the shrubs in big sagebrush communities in Yellowstone National Park. . . . . Francis J. Singer and Roy A. Renkin **201**

Soft sediment benthic macroinvertebrate communities of the Green River at the Ouray National Wildlife Refuge, Uintah County, Utah. . . . . Eric R. Wolz and Dennis K. Shiozawa **213**

Alpine vascular flora of the Tushar Mountains, Utah . . . . Alan C. Taye **225**

Ecology of *Celtis reticulata* in Idaho . . . . Ann Marie DeBolt and Bruce McCune **237**

Mimulus evanescens (Scrophulariaceae): a new annual species from the northern Great Basin . . . . Robert J. Meinke **249**

Morphological and host-symbiont studies of *Trichodina tenuiformis* and *Apiosoma campanulatum* infesting mottled sculpin (*Cottus bairdi*) from Provo River, Utah . . . . Ying Qi and Richard A. Heckmann **258**

Effects of horse grazing in spring on survival, recruitment, and winter injury damage of shrubs . . . . Dennis D. Austin and Philip J. Urness **267**

North American types of *Oxytropis* DC. (Leguminosae) at The Natural History Museum and Royal Botanic Garden, England, with nomenclatural comments and a new variety . . . . . . S. L. Welsh **271**

Notes

Saltation in snakes with a note on escape saltation in a *Crotalus scutulatus* . . . . . Breck Bartholomew and Robert D. Nohavec **282**

A trap for Blue Grouse . . . . Eric C. Pelren and John A. Crawford **284**

Book Review

Mountains and plains: the ecology of Wyoming landscapes *Dennis H. Knight* .... Kimball T. Harper **286**

No. 4—October 1995

Articles

Classification of the riparian vegetation along a 6-km reach of the Animas River, southwestern Colorado.................................. Gillian M. Walford and Willian L. Baker **287**

Additions to knowledge of Paleocene mammals from the North Horn Formation, central Utah .... Richard L. Cifelli, Nicholas J. Czaplewski, and Kenneth D. Rose **304**

Springtime movements, roost use, and foraging activity of Townsend's big-eared bat (*Plecotus townsendii*) in central Oregon..................... David S. Dobkin, Ronald D. Gettinger, and Michael G. Gerdes **315**

Names and types in perennial *Atriplex* Linnaeus (Chenopodiaceae) in North America selectively exclusive of Mexico........................... Stanley L. Welsh and Clifford Crompton **322**

New records of Scolytidae from Washington state ..... Malcolm M. Furniss and James B. Johnson **335**

Relative vulnerability to extirpation of montane breeding birds in the Great Basin... J. Michael Reed **342**

Grasshopper densities on grazed and ungrazed rangeland under drought conditions in southern Idaho...................................... Dennis J. Fielding and Merlyn A. Brusven **352**

Plant novelties in *Lepidium* (Cruciferae) and *Artemisia* (Compositae) from the Uinta Basin, Utah... .... Stanley L. Welsh and Sherel Goodrich **359**

Prey choices and foraging efficiency of recently fledged California Gulls at Mono Lake, California .... Chris S. Elphick and Margaret A. Rubega **363**

Notes

Hybridization between *Bufo woodhousii* and *Bufo punctatus* from the Grand Canyon region of Arizona................................ Keith Malmos, Robert Reed, and Bryan Starrett **368**

Reproduction in the banded sand snake, *Chilomeniscus cinctus* (Colubridae), from Arizona....... .... Stephen R. Goldberg **372**

No acoustic benefit to subterranean calling in the cicada *Okanagana pallidula* Davis (Homoptera: Tibicinidae)................................ Allen F. Sanborn and Polly K. Phillips **374**

Book Review

Natural history of the Colorado Plateau and Great Basin *K. T. Harper, L. L. St. Clair, K. H. Thorne, and W. M. Hess*... B. C. Kondratieff **377**

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GREAT BASIN NATURALIST Vol. 55, No. 4, October 1995

CONTENTS

Articles

Classification of the riparian vegetation along a 6-km reach of the Animas River, southwestern Colorado .... Gillian M. Walford and Willian L. Baker **287**

Additions to knowledge of Paleocene mammals from the North Horn Formation, central Utah .... Richard L. Cifelli, Nicholas J. Czaplewski, and Kenneth D. Rose **304**

Springtime movements, roost use, and foraging activity of Townsend's big-eared bat (*Plecotus townsendii*) in central Oregon .... David S. Dobkin, Ronald D. Gettinger, and Michael G. Gerdes **315**

Names and types in perennial *Atriplex* Linnaeus (Chenopodiaceae) in North America selectively exclusive of Mexico................ Stanley L. Welsh and Clifford Crompton **322**

New records of Scolytidae from Washington state .... Malcolm M. Furniss and James B. Johnson **335**

Relative vulnerability to extirpation of montane breeding birds in the Great Basin.. J. Michael Reed **342**

Grasshopper densities on grazed and ungrazed rangeland under drought conditions in southern Idaho .... Dennis J. Fielding and Merlyn A. Brusven **352**

Plant novelties in *Lepidium* (Cruciferae) and *Artemisia* (Compositae) from the Uinta Basin, Utah................ Stanley L. Welsh and Sherel Goodrich **359**

Prey choices and foraging efficiency of recently fledged California Gulls at Mono Lake, California............... Chris S. Elphick and Margaret A. Rubega **363**

Notes

Hybridization between *Bufo woodhousii* and *Bufo punctatus* from the Grand Canyon region of Arizona .... Keith Malmos, Robert Reed, and Bryan Starrett **368**

Reproduction in the banded sand snake, *Chilomeniscus cinctus* (Colubridae), from Arizona .... Stephen R. Goldberg **372**

No acoustic benefit to subterranean calling in the cicada *Okanagana pallidula* Davis (Homoptera: Tibicinidae) ..... Allen F. Sanborn and Polly K. Phillips **374**

Book Review

Natural history of the Colorado Plateau and Great Basin *K. T. Harper, L. L. St. Clair, K. H. Thorne, and W. M. Hess* .... B. C. Kondratieff **377**

Index to Volume 55.. **379**

3 2044 072 231 152